ZOOLOGISCHE STATION ZU NEAPEL

FAUNA and FLORA of the BAY of NAPLES

Monograph No. 35

ADOLF NAEF

CEPHALOPODA

Part I, [Vol. I,] Fascicle I

TRANSLATED FROM GERMAN

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ZOOLOGISCHE STATION ZU NEAPEL
Zoological Station, Naples

Fauna and Flora of the Bay of Naples

(Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte)

Monograph No. 35

CEPHALOPODA

by

Adolf Naef

Part I, [Vol. I], Fascicle I
with 62 illustrations and 19 tables

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Contents

Fascicle I

	German page	English page
FOREWORD	V	1

INTRODUCTION

	German page	English page
1. General considerations	1	8
2. Methods of systematic morphology	5	11
3. The form of systematic-morphological presentation	41	40
4. Preliminary systematic-morphological orientation	44	42
5. The recent genus Nautilus and the fossil Tetrabranchiata	55	53

MAIN SECTION

		German page	English page
CHAPTER 1.	Class Cephalopoda Cuvier	77	72
CHAPTER 2.	Subclass Dibranchiata Owen	90	84
CHAPTER 3.	Order Decapoda Leach	109	102
CHAPTER 4.	Suborder Teuthoidea Naef	135	125
CHAPTER 5.	Series Metateuthoidea Naef	149	137
	Appendix: Metateuthoidea Myopsida (d'Orbigny) Naef	165	151
CHAPTER 6.	Family Loliginidae Steenstrup	168	153
CHAPTER 7.	Genus Loligo Lamarck	193	179
CHAPTER 8.	Genus Alloteuthis (Naef)	207	193
CHAPTER 9.	Metateuthoidea Oegopsida (d'Orb.) Naef	224	210
CHAPTER 10.	Family Gonatidae (Hoyle) Pfeffer	242	226
	Genus Gonatus Gray	244	228
CHAPTER 11.	Family Bathyteuthidae Pfeffer	251	234
	Genus Ctenopteryx Appellöf	252	235
CHAPTER 12.	Family Enoploteuthidae (Pfeffer)	261	244
CHAPTER 13.	Genus Pyroteuthis Hoyle	269	251
CHAPTER 14.	Genus Abralia Gray	279	260
CHAPTER 15.	Genus Abraliopsis Joubin	285	266
CHAPTER 16.	Genus Thelidioteuthis Pfeffer	296	277
CHAPTER 17.	Family Onychoteuthidae Gray	301	282

Fascicle II

		German page	English page
CHAPTER 18.	Genus Onychoteuthis Lichtenstein	313	293
CHAPTER 19.	Genus Chaunoteuthis Appellöf	322	302
CHAPTER 20.	Genus Ancistroteuthis Gray	326	306
CHAPTER 21.	Family Octopodoteuthidae Berry	334	313
	Genus Octopodoteuthis Rüppell	334	313
CHAPTER 22.	Family Histioteuthidae Verrill	343	321
CHAPTER 23.	Genus Calliteuthis Verrill	352	330
CHAPTER 24.	Genus Histioteuthis d'Orbigny	362	340
CHAPTER 25.	Family Brachioteuthidae Pfeffer	370	348
	Genus Brachioteuthis Verrill	370	348
CHAPTER 26.	Family Chiroteuthidae Gray	376	354
CHAPTER 27.	Genus Chiroteuthis d'Orbigny	381	359
CHAPTER 28.	Family Cranchiidae Gray	392	371
CHAPTER 29.	Genus Galiteuthis Joubin	398	377
CHAPTER 30.	Genus Liocranchia Pfeffer	402	382
CHAPTER 31.	Genus Leachia Lesueur	406	386
CHAPTER 32.	Family Ommatostrephidae Gill	411	391
CHAPTER 33.	Genus Illex Steentrup	429	408
CHAPTER 34.	Genus Todaropsis Girard	438	418
CHAPTER 35.	Genus Ommatostrephes d'Orbigny	445	424
CHAPTER 36.	Genus Sthenoteuthis Verrill	455	434
CHAPTER 37.	Family Thysanoteuthidae Keferstein	463	444
	Genus Thysanoteuthis Troschel	463	444
CHAPTER 38.	Suborder Sepioidea Naef	473	454
CHAPTER 39.	Family Spirulidae d'Orbigny	505	485
	Genus Spirula Lam.	505	485
CHAPTER 40.	Family Sepiidae Keferstein	519	498
CHAPTER 41.	Genus Sepia L.	544	522
CHAPTER 42.	Family Sepiolidae Keferstein	564	543
CHAPTER 43.	Genus Rossia Owen	589	567
CHAPTER 44.	Genus Heteroteuthis Gray	595	573
CHAPTER 45.	Genus Sepiola (Leach)	601	579
CHAPTER 46.	Genus Rondeletiola Naef	629	608
CHAPTER 47.	Genus Sepietta Naef	640	619
CHAPTER 48.	Order Octopoda Leach	655	633
CHAPTER 49.	Suborder Polypodoidea Naef	675	651
CHAPTER 50.	Family Octopodidae d'Orbigny	681	657
CHAPTER 51.	Genus Octopus Lamarck	693	669
	Species of "Scaeurgus"	710	685
CHAPTER 52.	Genus Eledone Leach	716	692
CHAPTER 53.	Family Argonautidae Naef	725	702

	German page	English page
CHAPTER 54. Genus Tremoctopus Delle Chiaje	734	710
CHAPTER 55. Genus Ocythoë Rafinesque	749	725
CHAPTER 56. Genus Argonauta Linné	762	738

CONCLUSION

	German page	English page
1. Review of the evolution of the subclass including paleontological data	789	764
2. General conclusions	795	770
3. Technique	805	778
4. Systematic review and keys for determination	812	780
5. Bibliography		795
6. Subject index with remarks and list of figures		857
Plates to Volume I		879

V *FOREWORD*

The author considers the publication of this work as a modest harvest of long years of gratifying endeavor and unwavering perseverance amid the adversities of time. With a feeling which is equally remote from proud satisfaction and hopeless resignation, it is hoped that the work will stimulate further research.

This volume should mark a beginning, not an end. However, a stage has been reached and it would be of interest to review briefly the motivation and course of the study.

a. HISTORY OF PUBLICATION

At the invitation of Professor Dohrn, this work was begun in the spring of 1910. Originally conceived as a continuation of the monograph on Cephalopoda by G. Jatta (1896; Volume XXIII of this series), it was intended to deal with the anatomy, embryology, ethology and ecology of the Neapolitan forms with supplements to the systematics, which were considered as definitively established. Jatta had made extensive preparations for the anatomical part of his monograph, which remained unfinished owing to his untimely death.

It was not a simple task to complete the work in Jatta's spirit. As a morphologist in outlook, I had a particular way of thinking, as well as a theoretical concept which resulted partly from my own interpretations but was mainly influenced by the school of my Zürich teacher, Arnold Lang. I had no clear idea of the difficulties involved in executing the work conceived only in indefinite outlines, or of the large demands on time and energy required.

Already a preliminary examination of the most common Neapolitan forms showed that the anatomical studies of Jatta could not be used to construct an organically whole work: there could be no question of a rapid conclusion of this lengthy draft, as will be explained in Volume III. Systematics published at that time did not answer the requirements of modern science.
VI Repeated attempts to fill the gaps in Jatta's work resulted finally in a complete revision of the systematic part, until very little remained of the original. The following considerations will prove that these changes were indeed necessary.

It is not intended to criticize Jatta, whose highly meritorious work of 1896 with Merculiano's excellent plates stimulated wide interest in Cephalopoda. But it cannot be denied that he lacked the methodical mind to proceed in a planned way from the concrete object to an abstraction, and did not have the morphological education necessary for scientific interpretation of such manifold living forms. He did not attempt a critique or revision of the system, but remained faithful to tradition and relied on the authority of J. Steenstrup, whom he deservedly revered. The lack of a theoretical foundation is also evident in the lack of sharply defined diagnoses and keys for determination, which reduces the practical value of the work. This is, however, not the only reason that the monograph of 1896 is already largely outdated, while the energy expended could have produced a more lasting work. Later developments also had their effect: since 1896, thorough examination of expedition collections has considerably increased our knowledge of Cephalopoda. Among the renowned scientists who have made contributions in this field are G. Pfeffer, C. Chun, W. Hoyle and L. Joubin, assisted by the younger specialists S. S. Berry, A. Massy, G. Wülker, G. Grimpe, etc. Pfeffer (1912) published a detailed treatment of the Oegopsida; the 22 Mediterranean species of this group are today placed in 11 families, none of which were known to Jatta in their present definition, although three of his groups are still regarded as natural to some extent. A total revision of the Mediterranean forms and even of the entire class was imperative in view of the vast material accumulated (see also M. Sasaki, C. Ischikawa).

As early as 1912, Jatta's descriptions of the species were already inadequate, and their practical value to the nonspecialist decreased progressively. Jatta lists 38 species from the Bay of Naples, some of which are listed below with new determination, and Jatta's name is accompanied by a symbol which indicates the grounds for acceptance or rejection; N means that the species was correctly determined, but that the synonyms are invalid according to the rules of nomenclature; I means that the form is a young stage of another species, which Jatta did not recognize; Pl indicates a mixed species comprising organisms of valid, but different
VII species; F denotes wrongly determined species and genera; () indicates that the species also occurs under another name.

Jatta's names		Correct names
1. Thysanoteuthis rhombus	–	Thysanoteuthis rhombus
2. Ommatostrephes bartramii	N	Sthenoteuthis bartrami
3. Illex coindetii	–	Illex coindeti
4. Todaropsis veranyi	N, Pl	Todaropsis eblanae, partly Illex coindeti (male)
5. Todarodes sagittatus	N	Ommatostrephes sagittatus
6. Enoploteuthis margaritifera	N	Pyroteuthis margaritifera
7. Veranya sicula	N	Octopodoteuthis sicula
8. Teleoteuthis krohnii	(I)	Onychoteuthis banksi juv.
9. Teleoteuthis caribbaea	I	Abraliopsis morrisi juv.
10. Ancistroteuthis lichtensteini	Pl	Onychoteuthis banksi and A. lichtensteini
11. Doratopsis vermicularis	I	Chiroteuthis veranyi juv.
12. Entomopsis velaini	N, I	Brachioteuthis riisei juv.
13. Histioteuthis ruppelli	N	Histioteuthis bonelliana
14. Calliteuthis nevroptera	F	Ctenopteryx siculus
15. Sepiola rondeletii	Pl	Sepiola rondeleti, together with 8 other species
16. Sepiola aurantiaca	–	Sepiola aurantiaca
17. Rossia macrosoma	–	Rossia macrosoma
(18). Rossia palpebrosa	F	Rossia macrosoma
19. Heteroteuthis dispar	–	Heteroteuthis dispar

Jatta's names		Correct names
20. Sepia officinalis	–	Sepia officinalis
21. Sepia orbignyana	–	Sepia orbignyana
22. Sepia elegans	–	Sepia elegans
23. Loligo vulgaris	–	Loligo vulgaris
24. Loligo forbesii	–	Loligo forbesi
25. Loligo marmorae	N	Alloteuthis media
26. Loligo media	N	Alloteuthis subulata
27. Argonauta argo	–	Argonauta argo
28. Ocythoë tuberculata	–	Ocythoë tuberculata
29. Tremoctopus violaceus	–	Tremoctopus violaceus
30. Octopus vulgaris	–	Octopus vulgaris
31. Octopus macropus	–	Octopus macropus
32. Octopus defilippi	–	Octopus defilippii
33. Octopus salutii	–	Octopus saluzzii
(34). Octopus alderii	(I)	Octopus macropus juv.
35. Scaeurgus tetracirrus	F	Octopus tetracirrus
36. Scaeurgus unicirrus	F	Octopus unicirrus
37. Eledone moschata	–	Eledone moschata
38. Eledone aldrovandi	N	Eledone cirrosa

Jatta had a more or less complete knowledge of only a fraction of his species. This is evident from the frequent confusions: Todaropsis with a male Illex (Plate II, Figure 6; see p. 439*); "Enoploteuthis" with "Teleoteuthis" (Plate XII, Figure 24); "Ommatostrephes" with "Todarodes" (Plate XI, Figure 4); Sepia orbignyana (eggs) with S. elegans (Plate VII, Figure 13.21; Plate VIII, Figure 7.8). The adult of "Teleoteuthis krohnii," i.e. Onychoteuthis banksii, was confused by Jatta with Ancistroteuthis (Plate XIII, Figures 13—23). Furthermore, Jatta applied the name "Sepiola rondeletii" to a whole subfamily with 10 valid species, which I have placed in 3 genera; 4 of his species (Nos. 8, 9, 11, 12 of the above list) are juvenile forms of known Oegopsida, one (No. 14) is erroneously described as new, while another 10 (Nos. 2, 4, 5, 6, 7, 12, 13, 25, 26, 38) cannot be identified with the original descriptions and consequently bear incorrect names.

Thus, 2 of the 38 species (Nos. 18 and 34) have to be eliminated, while only 22 of the remaining 36 are correctly named. Another 4 of these names had to be changed (Nos. 35 and 36; Nos. 25 and 26) because they belong to later established or abolished genera. There thus remain 18 valid names.**

Later studies and observations have considerably increased the material of Mediterranean Cephalopoda. The Cranchiidae were entirely unknown to Jatta, although this family is common in Messina and was recorded in 1851 by Vérany (text-figure on p. 410). Galiteuthis armata (species 37) has been recorded with certainty, while Leachia cyclura (species 38) and Liocranchia reinhardti (species 39) are listed only with some reservation.

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* [All references to pages refer to those of the German original, which appear in the left-hand margin of the translation.]

** After serious deliberation, it was decided to apply all rules of nomenclature established at international congresses, although these are an unfortunate and needless burden on scientific work. But it should be pointed out in this context that it is senseless to deprecate valuable works of reference on the grounds of strictly fortuitous priorities, and thus make their use difficult. Fortunately, however, the well established generic names Octopus and Eledone were rehabilitated by Grimpe (1920). (See note on p. 696.)

Among the other Oegopsida, the following species have since been found in the Mediterranean (and occur accidentally in the Bay of Naples): Abralia veranyi (species 40), Calliteuthis reversa (species 41), Chaunoteuthis mollis (species 42), Thelidioteuthis alessandrinii (species 43), and Gonatus fabricii (species 44). In addition, empty shells of Spirula spirula (species 45) have been found, brought in by currents.

(IX)

Corrections to Jatta's plates

Plate	Figure	Correction
Plate II,	Figure 4	Eggs of Sepiola sp.; undeterminable! Not S. rondeleti!
	6	Male Illex coindeti, not Todaropsis! Figure 1 shows a female of the same species!
	7	Eggs of Sepia elegans, not S.orbignyana.
Plate IV,	Figure 5	Sepiola rondeleti or S.affinis.
	6	Sepietta obscura; not Sepiola rondeleti.
Plate V,	Figure 3	Undeterminable Sepiola (S.robusta?)
	4	Sepiola aurantiaca or ligulata, or Rondeletiola minor. Poor drawing!
Plate VII,	Figure 7	Eggs of Sepiola sp. (S.robusta?)
	8	Ocythoë tuberculata, male; not O. "catenulata".
	9	Octopus saluzzii; not O.macropus!
	10	Larvae of Octopus sp.; not Eledone!
	13	Egg of Sepia orbignyana; not S.elegans.
	15	Sepietta sp. or Rondeletiola minor; not Sepiola.
	17	Sepia elegans; not S.orbignyana!
	19	Octopus macropus juv., not O.alderi.
	20	Larvae of Onychoteuthis or Ancistroteuthis.
	21	Sepia elegans; not S.orbignyana.
Plate VIII,	Figures 7, 8	Eggs of Sepia orbignyana; not S.elegans.
Plate XI,	Figure 4	Third arm of Sthenoteuthis bartrami; not of Ommatostrephes ("Todarodes") sagittatus.
Plate XII,	Figure 24	Young of Onychoteuthis banksii; not Pyroteuthis ("Enoploteuthis") margaritifera.
Plate XIII,	Figures 13–23	Onychoteuthis banksi; not Ancistroteuthis lichtensteini.
	24–34, 42	Young form of Onychoteuthis banksi; not Teleoteuthis.
	35–41	Abraliopsis morrisi.
Plate XIV,	Figures 1–9	Chiroteuthis veranyi, young form; not "Doratopsis".
	10–15	Branchioteuthis riisei, young form; not "Entimopsis".
	16–30	Sepietta oweniana; not Sepiola rondeleti.
Plate XV,	Figures 11–21	Rossia macrosoma, poor speciment; not R.palpebrosa.
Plate XX,	Figures 19–26	Octopus macropus, young form; not "Octopus alderi".

Corrections to Jatta's text-figures

Page	Figure	Correction
p. 10,	Figure 9	Tentacle of Sepietta obscura (?).
p. 14,	Figure 20	Hectocotylized arm of male Sepietta oweniana. (Not S. rondeleti.)
p. 15,	Figure 22	Ventral arm of Abraliopsis morrisi. (Not Enoploteuthis.)
p. 22,	Figure 54	Funnel attachment of Ocythoë tuberculata. (Not Argonauta.)

The study of "Sepiola rondeletii" provided 9 species, in addition to S. rondeletii as characterized by Steenstrup, namely: 1. Sepiola steenstrupiana (species 46), 2. Sepiola ligulata (species 47), 3. Sepiola affinis (species 48), 4. Sepiola intermedia (species 49), 5. Sepiola robusta (species 50), 6. Rondeletiola minor (species 51), 7. Sepietta obscura (species 52), 8. Sepietta neglecta (species 53), 9. Sepietta oweniana (species 54).

Such is the range of forms discussed here, at least from the broad aspect. However, it should be remembered that each species appears in a surprising multitude of forms, this being expressed in sexual dimorphism (which will be described in the special chapters), and, especially, in development, although the discussion here will be confined to the postembryonic stages. Jatta was unaware of the typical course of ontogenesis in many cases because of scarcity of material or because he did not interpret the available data in morphogenetical terms.

The lasting value of Jatta's monograph rests largely on the excellent illustrations drawn by the artist Merculiano at the Station and reproduced with technical perfection by the firm of Werner and Winter in Frankfurt. Unfortunately, the use of these illustrations is reduced by the above-mentioned defects of nomenclature as well as by objective mistakes. A number of valuable and thoroughly applicable figures are named incorrectly, as shown in the table on the previous page.

IX b. ORIGINAL WORK

After my largely unpublished studies on the systematic morphology (anatomy and embryology) of Gastropoda, I began to study Cephalopoda in the spring of 1908 in Naples, resulting in a small publication (Dissertation, Naef, 1909) on the development of the coelom and central blood vessels. On my return to Naples in spring 1910 to continue the research and collect more material, the administration of the Station proposed that I continue the research begun by Jatta. I eagerly accepted, since this was the only way to fulfill a scientific assignment requiring long years of continuous research. I was able to complete the work between 1910—1916, thanks to the financial aid provided by the Zoological Station.

It was my original intention to write a single volume containing supplements to Jatta's work, and covering the systematics, anatomy, embryology, ethology and ecology of cephalopods, which at first I estimated could be
X completed in 3 to 5 years. It became clear after 3 years that the scope would be much wider, and although I had already completed a considerable amount of the planned preliminary studies, it was not yet a complete work. At my suggestion the original plan was changed and the work divided into several parts, the first part of which was to be completed and published. This was dictated by the need for a thorough systematic revision of the class. I was able to embark upon this enterprise because of the sound preliminary work in anatomy and embryology; the chapters dealing with morphology are the result of these studies. Furthermore, the systematic relationships described are also reflected in the internal morphology, as I was able to establish. However, mainly external characters in which the

practical systematist is mainly interested, are dealt with, although I was sometimes forced by the nature of the subject to describe also normally covered parts, for example, the mantle situs, which is in fact only a folded region of the primary body surface. It was also necessary to discuss the general morphology of the shell, which is originally an external element, and its relation to the soft body, as it provides important data for systematics. The shell has always been the main aid for practical determination of molluscs.

In autumn 1913, I began to summarize the studies for the first part and prepare it for publication. Most energy was probably expended in drawing the numerous figures, since I regard abundant illustration as the only adequate method of presenting the work, although the Station urged me to hurry, for valid reasons of its own.

Owing to limitations of time and money, further concessions had to be made during the final preparation of the first part. Since it became evident that an exhaustive treatment required more space than originally allotted, we decided to divide the work again. This division was carried out on practical considerations, as well as with respect to the nature of the material. Embryonic stages were to be described in a second volume, while the first volume was to cover only the postembryonic forms which are usually of most interest to the "systematist." Abnormal morphogenesis, regeneration and a number of theoretical considerations had to be omitted, together with a discussion of attempts to provide a dynamic analysis of morphogenesis. The rest forms a more or less compact whole in both form and content. A presentation confined to the body surface of free-living postembryonic stages proved on the whole to be well chosen. It was necessary, however, to include such readily accessible and frequently discussed hard parts as the radula and jaws. These are described here for
XI the first time from a systematic-morphological point of view and are methodically compared to determine their characteristics. Previous knowledge on this subject was fragmentary and inaccurate, and Jatta's data are hardly instructive.

Most of the work was carried out in Naples, where rich material was available, consisting of collections made regularly during my stay, eggs and young stages grown in the aquarium, specimens obtained with fish hauls during these years, and the preserved part of Jatta's collection. The best specimens are part of the collection of the Station. Due to the courtesy of some colleagues and with the cooperation of the Station, I was able to obtain material from Messina, where deep-sea forms are abundant. I am grateful to the renowned specialist, the late C. Chun, for giving me the opportunity of examining his collection in Leipzig for several weeks. G. Pfeffer was kind enough to invite me to examine the rich material in the Hamburg Museum of Natural History. During various visits, I was able to study rare specimens of exotic and Mediterranean cephalopods in Stuttgart, Munich and Vienna. Examination and drawings of this material provided me with first-hand knowledge of most recent genera. However, lack of both time and means precluded description and publication of the material.

Circumstances which kept me in Munich from August to October 1914 induced me, contrary to my original intentions, to begin studying fossil Cephalopoda together with recent species. For this I am grateful to the Munich paleontologists, especially Professors Dr. Broili and Rythpletz, who placed work facilities at my disposal during this period. As I had hoped, these

studies broadened and confirmed many assumptions and tentative concepts of the relationships between recent and fossil Cephalopoda. The publication of this incompletely worked-out material in the first part of this volume caused some confusion. The preliminary systematic treatment of the fossil forms (see pp. 46—50, 127—134) has to be thoroughly revised in view of my later work (1919—1922) which appeared in 1922 as a parallel monograph (Naef, Die fossilen Tintenfische. G. Fischer, Jena. 1922). In the following volume this is referred to frequently, and later quoted exactly (for example, pp. 473 and 671). My views of a rational synthesis between zoology and paleontology are presented in the work on fossil Cephalopoda. I would like to point out that marine research stations can make major contributions to paleobiological research, which cannot succeed without their help. As far
XII as cephalopods are concerned, the lack of a wider zoological cooperation is only too evident in the interesting and imaginative work "Paläobiologie der Cephalopoden" by O. Abel (1916).

This volume was written and the drawings finished on my return to Switzerland from September 1916 to May 1917. Two subsequent revisions were made: one for printing, begun in the autumn of 1919 and interrupted in the spring of 1921 (First Issue, pp. 1—147), and the second, when printing was resumed in January—April 1922. At that time the work was given its present form (from p. 148) with numerous addenda and corrections made necessary by recent research and publications.

It is my pleasant duty to express my gratitude to all those who have contributed to the preparation of this work. Above all, I am grateful to Prof. Dr. R. Dohrn, Director of the Zoological Station, as well as to the Station itself, for the large outlay involved. I received further financial aid thanks to the assistance of Professors A. Lang and K. Hescheler, of the Fiedler Foundation of Zürich, the Federal Commission for the establishment of the Swiss work desk at Naples, to the Education Department of the Canton of Zürich, to the Bavarian Academy of Sciences, which contributed 2,000 marks in 1917, despite wartime conditions, to the Prussian Ministry of Culture for the 3,000 marks placed at my disposal in 1917 at the request of the German Zoological Society, to the Prussian Academy of Sciences which contributed 5,000 marks in 1917 to meet printing costs, to the Foundation for Scientific Research at the University of Zürich which also granted 2,000 francs for printing.

My thanks also go to my personal friends and well-wishers for their help during the long years of work. I am much indebted to my colleagues at the Zoological Station for stimulating discussions, and also to Mr. H. Reiff of Zürich, Professor Dr. J. Schaxel of Jena, Dr. R. Gast of Komiza, Dr. J. Gross of Naples, Professor Dr. M. Rauther of Stuttgart and, last but not least, Professor Dr. P. Mayer in Jena.

Mr. V. Serino, the talented artist at the Zoological Station, deserves particular thanks for his cooperation in the preparation of many drawings and aquarelles (Plate XIX). This difficult task was hardly satisfying to his artistic talent, since it consisted of technical execution, copying and redrawing from sketches made by myself.*

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* The majority of the drawings are by the author.

1 *INTRODUCTION*

1. GENERAL CONSIDERATIONS

For a thorough understanding of a work not only its actual results but also its intentions must be considered. This requires some explanation.

Since my student years, the theory of evolution has been the focal point of my scientific interest. Long before beginning this manuscript I had made plans for a critical foundation and elaboration of this theory. The results obtained, some of which have been published, are to be seen mainly against this background. This monograph has been undertaken not because of a special interest in the Cephalopoda but within the framework of the general problems of biology and evolution. This is an attempt to obtain, on the basis of comprehensive systematic-morphological studies, new data on which the theory of evolution can be based and further developed. I began with the traditional assumption that the history of recent species can be reconstructed with the methods of comparative morphology. I hoped to be able to check this reconstruction by paleontological data and thus to obtain an insight into the factors and laws which determine the course of evolution. This original position was partly modified and clarified during the work. Similar studies have occupied the scientific literature of the last 60 years. However, most of the results obtained have been inadequate, as any phylogeneticist would admit; scientists in other branches have also stressed this, often with an air of superiority. Even the evolution of vertebrates is still insufficiently known despite the large amount of research. Among the invertebrates, I do not know of a single major group the phylogeny of which has been more or less satisfactorily clarified. It is therefore not surprising that the conclusions drawn from this inadequate knowledge are largely without foundation.

2 The basic concept of the theory of evolution (see p. 5) has developed from a hypothesis to a well documented theory the scientific validity of which has not been challenged. However, the "why" and "how" of the change of characters of a species is still problematic.

Realizing that my aim can and must be achieved by new and old methods I began to reconstruct at least a part of the phylogeny to such an extent that it could be considered as scientific fact. The variety of organic forms is so large that specialization is necessary if a thorough knowledge is to be obtained. Such a specialization can be obtained in two ways: either by "extensive" coverage of the entire field or by selection of a relatively large and promising group to be studied in detail and, if possible, extended. This "intensive" approach seemed more fruitful and my task was to choose a suitable object.

This object had to fulfill the following conditions:

1. The group to be examined from the standpoint of phylogeny had to contain a sufficient variety of form to permit manifold comparisons.
2. The embryology of the group had to be known for a large number of species of the different subgroups.
3. Paleontological evidence on the group had to be available in sufficient variety and completeness.
4. The group was not to contain too many species, since reliable information can only be obtained by personal examination.

Cephalopoda fulfill these requirements ideally,* perhaps better than any other group.

It is not my intention to discuss the relationships in general in the manner of the "phylogenetic conclusions" in most morphological works, the "scope" and "boldness" of which are often inversely proportional to the material examined. I attempted to make a detailed study of the entire group, its development and mode of life, in the hope of producing a unified and consistent picture of its evolution which would form the basis for general considerations.

3 My expectations were not entirely disappointed. The multitude of facts I established enabled me to reconstruct the course of evolution of the class comprehensively, if not without gaps. The picture obtained does not contradict the facts; the available evidence closely fits the theory in the simplest conceivable way, resulting in a satisfactory synthesis. As far as the obvious gaps are concerned, I shall try to define them clearly according to importance.

Another problem developed during the work. The difficulty of obtaining definite results in the field of phylogeny and comparative morphology became increasingly evident. This difficulty is due in part to the nature of the subject, but also largely to the lack of a suitable methodology. The basic suppositions and principles of phylogenetic morphology and evolution have never been critically examined and described, although their existence has long been subjectively recognized. Behind the "morphological instinct" and "tact" of many renowned scientists more good procedure can be found than was originally realized, whereas the "daring fantasies" of others barely conceal the lack of a good methodology. However, it is clear that even the best morphological studies would have gained in depth by the application of well-founded methodical principles.

It became clear that methodological insights can be obtained best by a combination of theory and serious objective research. I attempted to develop what seemed to me a well-chosen object into a source of methodological information for phylogenetic morphology. The results obtained, essential for a deeper understanding of the following special discussions, have been published in preliminary form in two papers (Naef, 1917, 1919, G. Fischer, Jena) and will be presented in a more comprehensive form in this monograph (see following chapter, p. 5).

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* Other suitable groups are the Gastropoda and Lamellibranchiata and possibly the Crustacea. I made such an attempt with snails (Naef, 1911), but later discarded it. On the whole, molluscs are a most suitable group, because of their well known paleontology and abundance.

To summarize: it was my aim to study personally and in the minutest
possible detail a complex but clearly defined entity of organic development
of form and to treat this group systematically, using the most exact methodo-
logical principles. This should establish the natural historical relationships
of the variety of forms in the most scrupulous manner and provide an insight
4 into the nature of phylogeny. This task could be fruitfully combined, in my
opinion, with a monographic treatment of the Cephalopoda of the Bay of
Naples. The success of this combination will be assessed at the end of the
volume.

The following parts of the work will deal with special problems that lie outside the scope of the above, in method and in subject. In particular, a methodological foundation of ecology is intended. Finally, a general revision of the biological concepts on the basis of the actual material is envisaged, although I fully realize that this is impossible to achieve under the present conditions.

5 2. METHODS OF SYSTEMATIC MORPHOLOGY

Contents: a. General orientation. – b. Idealistic morphology and the concept of the type. – c. Natural systematics of the species. – d. Definition of the typical and the morphological primacy. –e. Atypical similarities. –f. Idealistic morphology and phylogenetics. – g. Phylogenetic evidence. – h. General principles of phylogenetic variation. – i. Principles.

I have repeatedly expressed my views on the methods of systematic morphology, and a detailed treatment of the subject originally intended as part of this work has already been published.* However, the methodological views expressed are so closely connected with the present work and so essential for its understanding and evaluation, that an outline has to be given to preserve coherence.

This review will not be a summary of the work quoted but it will be expanded in many important aspects, particularly in order to deepen the understanding of subjects dealt with in the following special chapters.

a. GENERAL ORIENTATION

Phylogeny, which is the object of this discussion (p. 1), developed from the study of the characteristic similarities between the forms of life as expressed in the "natural system." Specific systematics has to be considered as the historical precondition of the concept of evolution in its modern form. Any logical, objective foundation of the concept of evolution must be connected with the system of organisms as a fact.

Systematics is not directly present in nature. It can therefore not serve as direct proof for the theory of evolution. The possible existence of a natural system is a problem in itself and the theory of evolution is an attempt to solve this problem in conjunction with others. This is done by the hypothesis that recent forms developed from one or several hypothetical primary species by the accumulation of inherited changes during evolution.

6 The following questions can be answered on the basis of this concept which has been established as a theory:

1. Is a natural system possible in its accepted form, i. e., as a genealogical tree branching into a variety of species (p. 12)? This is the main problem from which other questions follow:

2. How is it possible that the ontogenetic stages (p. 20) correspond to the systematic stages (p. 13)? (Parallelism of the successive stages of individual development and the "animal series" of natural systematics, p. 21.)

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* Idealistische Morphologie und Phylogenetik. G. Fischer, Jena. 1919.

3. How is it possible that the geographical distribution depends on the "systematic relationships"?

4. How is it possible that the sequence of systematic stages corresponds in general to the sequence of paleontological appearance (insofar as this can be established)?

The power of facts has gradually forced the thinking naturalist to accept the concept of a natural system. It became increasingly clear that there is an order behind the variety of phenomena which had to be interpreted. It was recognized that there is a close relationship between the different types of living forms, but the nature of this relationship remained at first obscure.

Natural systematics is generally identified today with phylogenetic systematics. This is quite wrong. Natural systematics is actually far older. Its foundations were laid even before the time of Darwin. Furthermore, natural systematics has created the basic suppositions of phylogeny as formulated in the above questions. Finally, it has not yet been shown how the phylogenetic (genealogical) relationships of the species can be arranged in a genealogical system without the idealistic views of the early morphologists. It is therefore important to show what natural systematics was before phylogeny.

The theory of evolution has a simple answer for the main question formulated above: natural systematics can be explained by the assumption that existing forms are the descendents of species which developed from a common ancestor in each group by continuous change and division of species, in a process comparable to the branching of a genealogical tree. The question how a natural system has been obtained is not explained, nor do genealogists deal with it in detail. Haeckel, for example, simply translated the results of the early systematics into a new language without providing evidence of his own (cf. below under f.) or checking the available information.

For decades, phylogenetics lacked a valid methodological basis and developed on the decayed trunk of a withering tradition rooted in the
7 idealistic morphology and the systematics of pre-Darwinian times. There was talk of systematic "tact" and morphological "instinct", terms which were felt rather than understood and consequently insufficient to form the frame of a science which required sound definitions and clearly formulated principles.

Phylogenetics and natural systematics deal with the same factual material, and although each has different basic concepts, both disciplines can be united in a single concept because their objects are so similar. I have therefore proposed the name of "systematic morphology" for this concept (Naef, 1913). This term has a good chance of being accepted because it uses well-known, readily understood words to define an inherently unified science. It is intended to show that there is an inner relationship between natural systematics and (comparative) morphology.

Our system is obviously morphological. On the other hand, morphology aims mainly at a logical order (i. e., "systematics") of phenomena by proving the existence of such abstract relationships between them as homonomy and homology. This is evident even to the pure practitioner. He will at least admit that the establishment of a natural system is a major task of "comparative" morphology, in any case a product of it. Consequently, these branches cannot be treated separately on methodological or factual grounds as has been done in practice. We shall now attempt to define the systematic morphology or morphological systematics which enabled Darwin and his followers to develop the theory of evolution. It will then have to be considered what this new theory has contributed to an essentially new orientation of the whole science.

b. IDEALISTIC MORPHOLOGY AND THE CONCEPT OF THE TYPE

Systematic morphology before Darwin was generally idealistic insofar as it went beyond mere descriptions of forms. The relationships between morphological phenomena, in which the discipline was so deeply involved, were of an idealistic nature and could not be conceived or expressed as actual relationships. Nature provided the material for a study, but the form (method) was evidently associated with the thinking subject, even more specifically than is usually the case with human knowledge.

The concept of the "type" is the foundation of idealistic morphology. This concept was first formulated by Goethe, who also defined the term "morphology" precisely. Since Goethe the concept has dominated the entire discipline. Unfortunately, the importance of the concept "type" has always
8 been taken for granted by the idealistic morphologist, and no attempt has been made to define it or determine its logical nature, resulting in an increasing confusion.

As we are unable to obtain clear information about the basic concepts and principles of idealistic morphology, we are forced to judge them by the efficiency of the discipline itself, to decipher them from the formulations in which certain statements are made, so to say, to try to revive the spirit of a dead language. Others will have to judge how far we have succeeded. It is not intended, however, to give a true picture of the knowledge obtained but to introduce order in this world of ideas. We shall also attempt to develop the established principles for the solution of our particular problems. We thus arrive at a system of concepts and basic principles which we call the *theory of typical similarities*.

The idea of the type developed from the comparative study of objects that showed the characteristic similarity of form which is highly characteristic of organisms. This similarity does not consist only in similarities of parts or properties, but applies to the whole of parts and their mutual coordination. Insofar as a definite relationship between two entities exists, we name it "typical" similarity.

A typical similarity exists between complex entities which consist of similar parts arranged in similar coordination.

Such a relationship is present in organic species in general and is expressed in forms, activities and adaptations. The relationship of forms, however, is mainly of importance for systematic morphology. An analogy can be made to similar geometric figures in which each part of a figure "corresponds" to a component of another. We find there "homologous" sides, angles and points. As in geometry, typical similarity is characterized by a *homology* of the parts.

Homologues are those components of different similar complex entities which show a similar coordination* to other parts of the same entities.

This is true of typical as well as geometrical similarities but in the latter a correlation can be expressed more exactly as a numerical proportion.

9 The analogy between typical and geometrical similarity can be taken even further. If two triangles have two equal angles, the wholes are similar — if organisms have typically similar parts, the wholes are similar. This is essential for the interpretation of fossils and, consequently, to paleontology as a whole. Fossils are not complete organisms, but only fragments which require reconstruction to be fully understood. This is done according to the principle of typical correlation, i. e. the experience that typically similar parts belong to typically similar entities. The natural system will be the foundation, as will be shown in the special part. The problems connected with the fitting of the parts into a whole are only outlined here; a more detailed discussion is not necessary at this point.

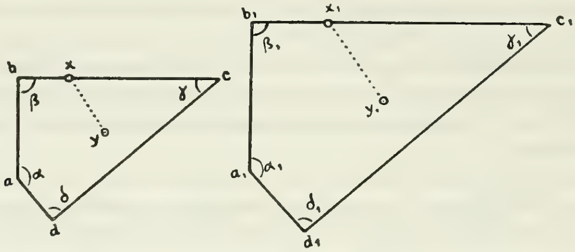

FIGURE 1. Analogy between geometric and typical similarity. The whole quadrangles are "similar," their parts "homologous." Compare the sides (a and a_1), the angles (β and β_1), the points along the sides (x and x_1), or those occupying a certain position in the interior (y and y_1).

Organic life presents a multitude of typically similar forms the abstract (systematic) association of which requires a common standard, a "tertium comparationis" (Goethe). Careful analysis of the morphological variety suggests that there should be an ideal form to which the individual forms would be related like the "single cases to the general law" (Goethe), that is, the ideal form should to some extent be the expression of not recognized objective necessities. This ideal form is the type. The question is how this ideal form is suitable for a centralized comparison of typically similar forms; or in other words, what is the relationship of the observed single forms to the ideal form.

We need here the term "metamorphosis," another basic concept of idealistic morphology. This term concerns the relationships between the

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* As will be seen later (p.11), this coordination can also involve a succession and thus become a time-space phenomenon, not only a spatial event. This covers the whole substance of the concept, but it cannot be based on individual or phylogenetic development (p. 20).

single forms. It had been observed long ago that typically similar forms can be arranged in a series or sequence which represents the successive stages of a process. Such a series of transitions shows a remarkable
10 analogy to the individual development* of organisms, and the transformation involved, but only in an abstract sense, was named "metamorphosis." This concept could be applied to all relationships of typical similarity, although in the German natural philosophy it assumed a vague and even mystic meaning which is of no importance here. It is easy to construct series of transitions (metamorphoses) between single forms, and these have been used to illustrate typical similarities (relationships of form) and to make them more striking and distinct.

The concept of such a metamorphosis can be connected with the idea of the type, and this can be defined as an abstract but naturally possible form from which a multitude of actually existing forms may have developed by the simplest metamorphoses. Thus, the actual form may be derived from the type, which can be reconstructed from the concrete form. The metamorphoses of the type are called "variations," a term which expresses a strictly ideal relationship of the actual to the ideal form. So defined, the ideal form resembles the "divine creative idea" of Agassiz or the theme of a set of musical variations.

The type has nothing in common with the idea of an ancestor or ancestral form. It is not a hypothesis nor does it exist in nature. Its actual existence is not postulated and is in fact an auxiliary concept, a methodical tool. Nevertheless, it should not be an arbitrary, unnatural or fantastic construction, in which case it would be of no value to the naturalist, to whom the nature of organisms has a very real meaning. The type must therefore have a "natural possibility."** Even if abstract, the type must be naturally meaningful and closely analogous to observed organisms. It is not a paper scheme without life and color.

These difficulties are avoided by deriving the type from the most similar and closely related structure, that is, the type should be constructed within a species, genus or family. Such an approach permits a detailed analysis of all compared facts, considering relationships and adaptations, so that the result will be a lively, clear picture. The ideal type represents a complete, naturally possible, if only abstract, organism which is the most characteristic and dominant of objects studied. As the type resembles the single
11 forms in as many characters as possible (the metamorphosis must be simple), it is represented by the same concept which has the same definition (diagnosis) as the single forms. The type of all snails is a snail and that of all vertebrates a vertebrate. In the circle of related forms, however, the type occupies a prominent or central position from which the individual forms are derived and morphologically interpreted. We name this the morphological primacy of the type. The term "atypical" refers to what is in contrast to the type.

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* It has been since observed that individual development does not involve the creation of a desired form on rational grounds. Even superficial observation shows a connection of widely different morphological relationships by actual transformation which reveals the true relationships or bridges the contrast between them by transitions.

** We require this also of transitional stages, i. e., all auxiliary concepts which assist the understanding of organic formation (Naef, 1917, p. 21).

The type cannot be a static, immutable or unique form if it is to approximate living nature. Each organism develops, and the typical organization also has its development. Among the higher animals (which will be discussed later) the type invariably is an ontogenesis which can be demonstrated by a sequence of stages. Only in this form can it conform to the strictly practical requirements demanded by systematics. All basic morphology is therefore embryology.

The concept of homology should also be applied to the natural parts of ontogenesis, insofar as they are stages. In a comparison we speak of homologous stages, adding the time correlation of spatially defined conditions (p. 8) to the concept of typical similarity. Homologous are those conditions or stages of typically similar ontogeneses which occupy corresponding places in the course of variation of form (see also p. 20).

In the final analysis, however, typical similarity does not apply to the ontogenesis of individual organisms but of entire species, in which the variety of forms is often represented by a multitude of organisms of typically different structure (polymorphism). Higher animals, for example, have two sexes, which together constitute the species. Comparison of such species yields a sexually differentiated type representing stages, as in real species, first the common characters of all individuals and then the specific characters of each sex. Thus, the type concept is generalized sufficiently for this work, the immediate aim of which is the systematics of the dibranchiate Cephalopoda.

c. NATURAL SYSTEMATICS OF THE SPECIES

The concept of type is the methodical basis not only of systematic morphology in general, but of the systematics of species. This term is generally interpreted in relation to species, but it may have also the wider meaning of an abstract order of phenomena (p. 7).

We must define here the concept of species, which is the object of this systematic discussion. Many confusing statements have been made about
12 the nature of the species, although the matter is quite clear. Species are natural communities of reproduction of known organisms. Ancestors and descendants, blood relatives, fertile males and females belong to the same species. Nothing else.

This relationship may be substantiated in practice by morphological similarities or ruled out by morphologic differences. This, however, has nothing to do with the concept itself, since there is no morphological concept of species. To distinguish between different species is to consider them as separate communities of reproduction; if we unite them into groups we deny this separation, regardless of the special reasons. We shall not discuss here the difficulties of applying the above rule (e.g., restricted fertility of different varieties, etc.).

The systematics of species is based on a study of their typical similarities, which results in the formation of a "group" or "systematic category" composed of species for which a common type can be established. It becomes evident that the typical similarity or relationship of forms is graded in the sense that smaller groups can be united into larger groups and these into still larger units. This follows the same basic principle in that the special types are derived from more general types.

The graded variety of forms within a larger group of organisms can thus be reduced to the relationship between their respective types. This relationship can be easily expressed graphically by the genealogical tree, the most perfect picture of natural-systematic relations. The potentialities of the genealogical tree are shown in the following example.

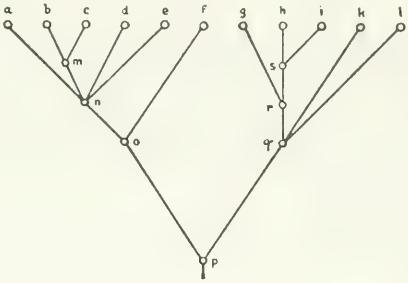

FIGURE 2. Ideal genealogical tree with an indication of the assumed types.

Figure 2 represents the genealogical tree of a number of species. There are 11 species (a—l), each capable of producing a number of special cases. b and c belong to the common type m; a, m, d and e belong to n; n and f belong to o; q belongs to p. All the species are special cases of their respective types. p is the prototype of the whole group. Starting from p,
13 we reach c via o, n and m, i. e., by a series containing 5 types (p, o, n, m, c).
I use the term "systematic sequence" for such a combination (p—o—n—m—c). The stages of the systematic sequence cannot be omitted or overlooked in a morphological study. For example, the morphological relationship between c and p can only be established by m, n and o, that between c and h only via p, q, r and s in addition to the above stages. The only way to achieve this is if the typical relationships are thoroughly worked out, i. e., if the genealogical tree is the result of a comparative morphological study. There is no networklike relationship as stated by J. Hermann (1783), and no convergence of sequences of stages into a single type.

The systematic sequences proceed from "lower" to "higher" forms, from the general to the particular, but also at the same time from higher to lower units of the system. We speak, therefore, of preceding and of following stages. In addition to and based on the valid range of the type in the genealogical tree, these stages express sequences within which one can distinguish between superordinate and subordinate arrangements.

The systematic sequence is, then, a particular case of a transitional series (p. 9) and illustrates a metamorphosis of a special meaning already to the idealistic morphologist, not only to the phylogeneticist. (A mere transitional sequence may also be the sequence a—b—c—d—e—f—g.) This is so because the systematic sequence shows the major morphological relationships by which a given structure can be traced back to remote, generalized ancestral types of organic form. Naturally, the completeness of these transitional series depends directly on the existing and available variety of forms. If species g is absent in the genealogical tree in Figure 2 stage r in the series p—q—r—s—h cannot be determined, because this stage results from a comparison between the types g and s (p. 10).

It might be assumed that the variety of organic forms could be classified also without the apparatus of typical relationships. This is true to some extent: the systematist often uses diagnoses instead of types. A correctly formulated diagnosis is a simple definition which expresses the concept, i. e., the common characters of a systematic unit. A definition contains the higher category ("genus") together with the specific characters ("differentiae specificae"), providing in each case a complete list of the characters common to all members of the group. Some of these characters are contained in the higher category, others are the specific characters. Nothing else belongs in the diagnosis.

The diagnoses form a collective, abstract structure in which each species has its place. They correspond closely to reality, since the similarity of characters is apparently more or less real, and identification does not require any special logical apparatus. Diagnoses can express graded morphological relationships and create a system of organisms which agrees
14 largely with that based on typical relationships. Diagnoses are simpler and would therefore be preferable if they could perform the same task just as efficiently. This is not the case, however.

The transition from lower to higher units of the system often involves a rapid loss of common characters. As a result, the highest units may show no common characters, although the typical relationships remain and permit a morphological characterization to the highest units. No useful diagnosis can be given for all molluscs, nor for some of the subgroups like the Gastropoda, because no common characters exist (Naef, 1919, p. 23). The justification of these categories is based on the idea of the ancestral or ideal form (see Introduction, p. 4). Although rather vague, this idea can be constructed methodically to a certain point.*

On the other hand, there are not natural, i. e., incorrectly established, groups which can be defined by a well-worded diagnosis. An example are the "Myopsida" of d'Orbigny as will be shown in Chapter V. This group has its common characteristics, in contrast to d'Orbigny's "Oegopsida." The diagnostic characters are, however, typical for all decapods (including the Oegopsida) and are therefore not applicable as characters for the group. Furthermore, the Myopsida are divided into 2 subgroups (Naef, 1913, p. 461), one of which (Loliginidae) agrees with the Oegopsida in some special characters (gladius), and together with the Oegopsida stands in contrast to the type of the other (Sepia-like) subgroup. To distinguish or associate species on the basis of common characters is often unnatural. Such an approach may be preferable for a catalogue of species, but not as the basic principle of scientific systematics.

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* K. Hescheler (1901) states with respect to the Gastropoda that the genus Pleurotomaria answers all requirements of the ancestral form, so that the systematic homogeneity of the group in terms of our principle is demonstrated. At any rate, the type of Pleurotomaria probably does not include the symmetrical fossil (Paleozoic) Bellerophontidae (cf. Naef, 1911).

The artificial nature of diagnostic distinctions and associations is also evident from the fact that they depend entirely on the state of knowledge about the species at the time they are formulated. It is therefore not certain that a given formulation is definitive. Discovery of a new species may invalidate the existing diagnosis or result in quite unnatural distinctions. Mammals without teeth, fish without scales, snails without shell and stags without antlers have been found, and the diagnoses would have to be changed to accommodate these "outsiders." Despite their striking deviations, these forms are classified on the basis of a principle different from any similarity of characters, which shows that this principle has been tacitly if not openly accepted.

The obvious disadvantages of the system of diagnoses cannot be corrected by dividing the characters into "essential" and "nonessential." Such a distinction is arbitrary and cannot be used methodically.

The diagnosis has not the same function as the type in another sense as well. The type does not only provide the principle of unification of a group of forms, but determines, by centralization of the morphological comparison, an order of ranks by regulating the sum of morphological relationships (Principle of Systematic Procedure, p. 19). In the diagnosis everything is equal.

As stated by Goethe, the type is learned from nature, and is natural despite its idealistic raiment. The methodically derived formulation is obligatory, based on knowledge which will not be upset by the first puzzling fact. If a new species does not fit into the ideal framework of a family, it obviously belongs to another, possibly wider circle of forms which does not affect the original content and composition of the family.*

Conventional systematics with its hierarchy of classes, orders, families, etc. should express the typical relationships of the genealogical tree. This is generally accepted, irrespective of whether the tree is ideal or shows actual descent. The translation of these relationships into conventional terms has resulted in many difficulties which have practical importance if the relationships have to be formulated and systematized. The following is an example.

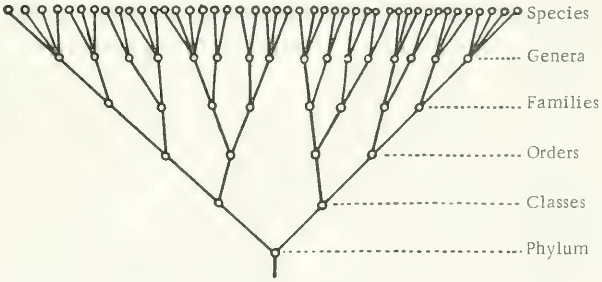

FIGURE 3. Ideal genealogical tree and its transfer to the conventional systematics.

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* The absolute determination of the rank of groups is not natural but fulfills only a practical need. Consequently, it can be changed to fit new species. Such a change does not detract from the value of the type or alter the composition of groups.

Figure 3 may represent a larger group of animals. Translated into systematic terms, it easily leads to phylum, classes, orders, families, genera and species. Real genealogical trees, however, are often quite different:

16 1. The number of branching points (types) is often greater or smaller than the number desired or needed to obtain systematic clarity. In the first case this is solved by the use of "intercalated" units such as subgenera, subfamilies, suborders, etc. These are often insufficient, and it becomes necessary to add tribes, series, and other units without definite rank. If the number of branching points is too small, "empty" groups have to be used, e. g. families with a single genus, genera with only one species, etc. Such units only fulfill the need for symmetry, clarity and abstract opposition but not the inner need for a systematic relationship. Where there are too many branching points it may not be necessary to give a diagnosis for each unit, especially with respect to subgenera, subspecies and other small categories — but not for species! (Naef, 1919, p. 48).

2. A much more serious difficulty arises when the types or closely related forms actually exist and have to be inserted in the system. To the phylogenetical systematist these forms are just as inconvenient as they are instructive, since they cannot be placed as species in the conventional framework of the system, at least not without compromise. They would have to be coordinated to the other species and at the same time superordinated. A truly adequate form of a natural system should have a well defined place for the existing types. It should also express the gradation and sequence of morphological relationships. This can only be achieved by a genealogical tree.

3. The above problem is connected with another difficulty. We are dealing not with ancestral forms which do not exist but with closely related forms which share some typical characters with the ancestral forms, in contrast to other forms, which are characterized by a common deviation which is typical for them. As the following examples show, we are dealing with a central group from the type of which the type of a divergent category has to be derived. It is an unconscious convention in systematics to coordinate the whole central group to that derived from it, provided that the type of the latter is more or less contrasting and well defined. Such an approach, however, would be an encroachment on the principle on which the system is based. It would be necessary at least to characterize the derived groups distinctly. To be consistent, the central group would have to be divided into as many branches as can be coordinated to the derived group. This would impair the clarity of the system and necessitate major changes in the existing system, which should be avoided as far as possible.

Thus, the Dibranchiata are placed opposite the "Tetrabranchiata" which, on close consideration, actually form the central group of the former and are divided into several subgroups. With the exception of the Endoceras-like forms, these subgroups have to be assumed to be derived from a common ancestral form, which we assume to resemble Orthoceras.
17 However, the same ancestral form belongs to the Dibranchiata as well, while there is no justification to connect the various Nautiloidea and Ammonoidea on the basis of similarities that are not valid for all Cephalopoda (see Introduction, p. 5). Hence, the Dibranchiata would have to be coordinated with the natural, questionable subgroups of the Tetrabranchiata.

In reality, one often has to deal with a number of coordinated groups arranged in a systematic sequence where each group represents the core group of another (i. e. the "following") group (p. 13). If this relationship has to be preserved, it must be specifically formulated by a) a clear statement to this effect and b) a definite sequence. The natural orders of Gastropoda may serve as an example[*] (Naef, 1911), although the relationships among the classes of vertebrates are better known.

Fish, Amphibia, reptiles and birds are not branches of equal rank on the genealogical tree. Actually, in the above sense, each class is the central group for the following class. Thus, the type of the birds is derived from that of the reptiles, the latter from that of the Amphibia, and this finally from the type of the fishes. Furthermore, the major groups of fish (Selachii—Dipneusti[**]—Ganoidei—Teleostei) show essentially the same relationship, although their mutual relations are still highly uncertain.

Introduction of these relationships in the genealogical tree gives the following results. The umbelliferous pattern (Figure 3), which is directly translatable into systematic terms, is often replaced by a horsetail pattern in which the steplike modification of the original forms is more evident. This is particularly the case with the Gastropoda and Vertebrata (the phenomenon was first observed in the vertebrates). It is a survival of the early concept (of Bonnet?) of the "animal series," which contains a correct view.

The system of animals prevailing today is not strictly like a genealogical tree of the variety of forms (Figure 2). It represents a rather steplike order (p. 13) in which no attempt is made to separate the various heterogeneous principles involved. A natural as well as practically useful system must combine the sequence of systematic or phylogenetic stages with the tree pattern in which the types or ancestral forms are divided. All accepted systems have done this without discussing the matter in principle.

Principle: The following systematic categories should be coordinated as of equal rank: a) subgroups derived by divergent variation of a type, or
18 b) all species placed before and after two successive stages of the genealogical tree, provided there is a distinct morphological contrast between these two stages. In the latter case the sequence is important and must be explicitly formulated. If such a series continues, the contrast can always be used to establish and distinguish successive steps. Examples of such contrasts are Tetrapterygia—Tetrapoda, Anamnia—Amniota, Diotocardia—Monotocardia.

Whether types or diagnoses are used to introduce order into a variety of forms, a thorough analytical treatment is indispensable. Thus, the ontogeneses are divided into stages in which we distinguish and compare single characters. In complex organisms it is advisable to follow the development of well defined parts through the sequence of stages, the parts in question being considered as units of lower rank[†] which possess a relative independence. To arrive at a diagnosis one merely has to find the common characters, and this does not require any special logical equipment. The common characters of a group naturally also apply to the type. To determine the type, however, the different but homologous characters have also to be compared. This analysis involves differentiation, evaluation and consideration of the individual elements. It attempts to distinguish the typical from the atypical and to obtain a picture of the type as a whole by determination of the typical in the individual.

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[*] The groups (orders) of Gastropoda (Belleromorpha, Zygobranchia, Trochomorpha, Neritacea, Ctenobranchia, Opisthobranchia) are staged groups like the classes of vertebrates.

[**] Including the Crossopterygii!

[†] "Morphogeneses." See Naef, 1917, 1919.

d. DEFINITION OF THE TYPICAL AND THE MORPHOLOGICAL PRIMACY

The widespread practice of relying on "morphological instinct" in differentiating between typical and atypical characters should not be applied, as such an approach never resolves controversial problems. It is also quite possible to formulate clearly the criteria for such an evaluation. A true science cannot rely on emotion to solve its basic problems and at the same time maintain a soul-destroying objectivity. Yet an emotional concept does assist the morphologist. There is a definite union of ideas between esthetics and morphology which deserves more thorough study.

The type occupies a prominent place within the "group" or systematic category which it characterizes. This position may be named the "morphological primacy" of the type. The question is whether this primacy applies also to separate characters and complexes of characters which diverge from the type or whether the type merely shows average values. The latter appears to be more probable. A review of the morphological literature
19 shows that there are numerous animal forms which occupy a peculiarly dominant place in their respective groups but which also show a markedly eccentric character (Pleurotomaria among the Gastropoda, Nautilus among the Cephalopoda, Amphioxus among the Chordata, Hatteria among the reptiles, etc.). These examples show that morphological primacy does apply to certain individual forms, although this concept is not clearly defined. Furthermore, the relationship does not cover all characters of these forms but only an important part of them (p. 23, IV).

Morphological primacy is based on three major criteria: the ontogenetic, systematic and paleontological precedence.

I. **The primacy of systematic precedence** states that a character typical for an entire group of forms has to be considered also as typical for the subgroups, provided it occurs in them. As noted on p. 13, the type of the larger group is defined in the genealogical tree as a systematic stage which precedes the type of the subgroup. The characters of the larger group appear in the subgroup as a morphological primacy with regard to other characters. Thus we arrive without difficulty from the higher type to the individual forms. It follows, however, that the lower type must be defined in the same manner. This principle follows from the nature of graded typical relationships. Just as the content of the wider diagnoses passes (in the form of a higher concept) into the diagnoses of the subgroup, the higher type determines the subordinate type and the preceding stage the following stage. This is an expression of the inherent connections in a system of organic forms based on typical similarity.

II. **The primacy of ontogenetic precedence** follows from the general experience that the degree of similarity between morphologically related organisms increases at the beginning of development. This statement can naturally be extended to the type. To use J. Müller's expression: juvenile stages of different animals resemble the common type more closely the younger they are. This formulation needs qualification before it can be considered as a rule, because there are apparently many exceptions, especially in larval and embryonic organs. The larvae of Diptera, for example, differ externally much more than the adults.

The nature of these exceptions gives the explanation. Larval and embryonic organs are complete structures, not early stages of parts of the adult animal. The rule deals only with these early stages and their relation to the later condition. This is not a question of mere precedence or even absolute age, but only an observation that certain structures are the early stages of others which develop from them later. The morphological stages which occur during ontogenesis always resemble the type more closely than the stages which later develop from them.* In this formulation, there are no exceptions to the rule (I have not found a single exception in the literature or in the very large material I examined). A more detailed discussion of this principle cannot be made here. Numerous examples may be found in the special part.

It is seen from the above that embryology is very useful to systematics since it provides a large number of diagnostic characters. It is of particular interest that embryological phenomena take a different course although they start from identical early stages. It is, however, impossible to distinguish directly between these divergent trends, between typical and atypical characters, on the basis of the morphological primacy of the preceding stages. This would require further auxiliary considerations. The question arises whether the relationship to the typical early stage permits an evaluation about the following stages.

An objection to the above statement must be answered here. The similarity of the early stages of homologous structure to each other is due not to a lack of specific characters but to the existence of morphological elements which are in sharp contrast to those of the later stages. For example, typical juvenile stages of lungfishes (Crossopterygii) have external gills like the larvae of Amphibia, which they resemble in other respects as well. These juvenile organs later disappear in both groups.

There are species in which the typical juvenile states persist completely, i. e. only some details being changed, while the position and arrangement of the major components remain the same. In others the general "plan" changes radically. The primacy of ontogenetic precedence can be applied to the case in which adult characters developed directly from the typical juvenile condition.** Such a case can be defined as a similarity of style between adult and young. Quite different are cases in which the typical juvenile condition persists ("neoteny"; Naef, 1919, p. 31); further development and modification of certain parts is here simply inhibited.

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* I have previously attempted to formulate this qualification by the concept of morphogenesis (1913, 1917, 1919).

** In comparative anatomy certain types have been described as embryonic; this term has also been applied to fossil groups (cf. Broili-Zittel, 4th ed., 1915, p. 11).

The similarity between the early states ("anlagen") of some structures has often been considered as proof of their homology, and this is quite correct. The principle may be stated that if two structures are homologous in the state of "anlage", they must be homologous later also. However, this does not mean that the concept of homology can be based on development, as is generally done. This would be a "petitio principii." We are dealing only with the homology of "anlagen", which can be directly demonstrated to prove the homology of the later structures which develop continuously from them.

We must now consider the old theory of the "parallelism between ontogenetic and systematic sequences" (in my terminology) or the "parallelism
21 between embryology and the animal series," in the formulation of Meckel and the idealistic morphologists. This is an extension of our principle which states that the preceding stages are closer to the type of the next systematic group or stage than the stages which develop from this type, but the farther back one traces the ontogenetic sequence, the larger the number of forms included in this approximation. K.E. von Baer clearly formulated this observation in stating "that the earliest stage of each organism shares the greatest number of characters with the earliest stages of all other organisms; that at a slightly later stage the organism is structurally similar to a corresponding stage in a smaller group of organisms; that in each successive stage the embryo acquires new characters which distinguish it from an ever increasing number of groups of other embryos which were previously identical with it, thus progressively reducing the group of embryos that still resemble it; in this manner the group of similar forms shrinks to the single species to which the embryo belongs."

Translated into the concepts used here, this means that morphogenetic processes pass more or less closely through the systematic stages which lead to the species of the organism because the occurring forms are characteristic or typical for ever smaller groups of organisms. This shows the enormous value of embryology for natural systematics; if the above law is applied in reverse, an assumed systematic relationship can be checked against the individual development.

Ontogenesis shows a real progress from lower (usually simpler) to higher (more complex) forms and establishes a natural connection between them. This gives solid support to the view that the variety of organic forms is internally coherent and that a ("natural") system truly represents the natural relationships (p. 6). Systematic morphology thereby gains consolidation and this explains the deep interest in embryological studies, from the beginning.

III. **The primacy of paleontological precedence** was not actually established — or at least not clearly formulated by the idealistic morphology. This would have presented the variety of organic forms in a historical perspective. Yet even a strictly idealistic morphology could not have ignored the fact that geological evidence shows a distinct precedence of the typical and succession of the atypical. Thus, the Tetrabranchiata preceded the Dibranchiata, the Nautiloidea preceded the Ammonoidea, fish the Tetrapoda, etc. The idealistic morphologist was well acquainted with the facts of this progress.

22 Haeckel* pointed out that the paleontological sequences correspond strikingly to the systematic and ontogenetic sequences (Reihe der Wirbelklassen, p. 17). However, the paleontological sequences are generally less consistent and complete than the systematic sequences (p. 13). By contrast, ontogenesis with its complete series of stages demonstrates the metamorphosis of the organisms as a real process, and shows the natural connection between the different stages. The gaps in the paleontological picture, however, should not detract from its value since they are due mainly to the lack of preserved material. Thus, both ontogenetic and paleontological data strongly support our systematic-morphological concept. Mainly because of them the "natural system" appears as a formulation of facts which must and can be explained, as pointed out in the Introduction (p. 5). The theory of evolution provides a causal link between the three series of phenomena. It also reduces the three kinds of precedence to a cause and effect relationship.** The systematic-morphological way of thinking then appears as causal thinking in disguise.

In the final analysis, the systematic-morphological way of thinking may find here its deeper justification, and one is tempted (like Haeckel) to discard the methodological apparatus of idealistic morphology and to adopt instead an essentially historical viewpoint, which the proponents of "phylogenetics" have not done. This is indeed my intention. However, I cannot produce at present a valid equivalent to the principles of idealistic morphology. The principles of historical order of the variety of organic forms can only be based on the laws of phylogenetic development, and these have not yet been clearly formulated. † On the other hand, a methodology of idealistic systematics is partly available and the rest we could construct by elaboration of existing views. Our particular purpose can thus be achieved in a logical manner.

Let us return to the morphological primacy. The question arises whether the series of principles which determine the morphological primacy can be supplemented by the inclusion of further elements. In my view, principles
23 of equivalent rank cannot be established any more but it is possible to formulate and tacitly apply some auxiliary principles based on the three basic ones.

IV. **The primacy of typical correlation** means that among comparable states of typically similar organisms, the higher rank in the definition of the typical belongs to those which are naturally correlated to others that are already established as typical (Naef, 1919, p. 30).

V. **The primacy of complete development.** If two organisms are typically similar but some of them lack homologous structures or their final stages, the organisms in which these parts are fully developed rank higher in the definition of the typical (cf. Naef, 1919, p. 31; also the chapter on the genus Sepiella in the special part, particularly with regard to the absence of luminous organs).

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* Haeckel considers the threefold parallel of systematic, embryological and paleontological sequences as... "one of the greatest, most important and most wonderful phenomena of living nature."

** The nature of ancestral forms is the "cause," while the nature of the descendants, which depends (at least in part) on that of their ancestors, is the "effect."

† The morphological primacy would have to be replaced by the historical (phylogenetic) priority, for which similar criteria should be established (Naef, 1919, p.51).

VI. **The primacy of monomorphous development of homonomous parts.** Parts of the same individual are often typically similar ("homonomous"), and we will attempt to construct a type for these parts as well. This does not involve the establishment of an ancestral form, but only an ideal basic form. The abstraction made in connection with a single part, however, will be applied to the whole. For example, having established that the basic form of the limb of a lower crustacean is a biramous leg, one may assume that such an animal could be completely equipped with biramous legs. A comparative study of Crustacea suggests that such an ideal form is the type, and we ask whether this way of thinking might not have a more general justification. This conception seems fruitful and firmly based in the spirit of idealistic morphology. Thus, wherever a structure is seen to be polymorphous in the same individual, it is possible to visualize an ideal form in which this structure is monomorphous, i. e. expressed in a uniformly typical manner. This ideal form often represents the general type of an enlarged group of forms, that is of a preceding systematic unit, and we are inclined to give this structure morphological precedence also if it is unknown (extinct?). We therefore consider the construction of ideal forms with monomorphous parts as a heuristic tool of systematic morphology. The structure observed can be derived from such ideal forms according to the principle of the division of labor. Applied in reverse, our way of thinking shows the primacy of undifferentiated polymorphism over differentiated polymorphism.

Principle: the polymorphous structure of homonomous parts in an organism (or in individuals of a group) can be reduced to a monomorphous structure in which the typical structure is replaced by an atypical structure. Uniformly constructed homonomous parts are to be considered as primary within a systematic category (numerous examples may be found in the special part).

24 VII. **The primacy of monomorphous structure in individuals of the same species.** Not only individuals of different species and parts of the same individual are typically similar, but also individuals of the same species. The degree of such a similarity may be so great that one can speak of morphological identity and not proceed to the construction of a type, which each individual apparently represents by itself. However, this is not always the case. The polymorphism of species is well known. All textbooks stress, for example, the typical similarity between polyp and medusa, or derive the form of the medusa from the type of the polyp, doing so by postulating the existence of a more remote ideal form of the species in which all individuals are uniform. This is in fact the assumption of the morphological primacy of the monomorphous state. Polymorphous species are always considered descendants of monomorphous species.

These considerations can also be applied to sexual dimorphism. The dimorphism of sex cells is undoubted typical (general), at least for all the Metazoa. Monomorphism of these cells will have to be placed in the remote past to the most general forms of dioecious reproduction. It is different with respect to the so-called secondary sexual characters. Here we will have to look for a more closely similar monomorphous prototype which is represented by the basic form of the genus or family in some cases, by that of the class or phylum in others. More information can be obtained by a special comparison of forms. A particular dimorphous character can often be traced back to a monomorphous character without assuming a monomorphous structure of the respective type. An example is the hectocotylization of decapod Cephalopoda, which affects different arms. This could occur in the ancestral form but not in its specific structure.

Principle: If the individuals of one species (or the species of a group) show a different structure, this condition has to be traced back to a monomorphous state which, if it exists, should be considered to have morphological primacy in a systematic category.

Neither of the above principles means that the simpler state is the starting point of morphological variation (p. 10). Not all complex states can be traced back to simpler ones, if our basic concepts are valid. Many complex types of organizations undergo a successive series of simplifications which leave a distinct mark in ontogenesis. Examples are the development of the larvae of Ascidia, Sacculina, parasitic snails, etc. The metamorphosis of individual parts often follows a descending path. There are blind forms among vertebrates and cephalopods, the eyes of which are primarily typically differentiated. A principle of progress cannot be taken into consideration in the evaluation of typical similarity. "Lower" forms (p. 13) are not always simple (p. 21).

25 The last 4 principles (pp. 22—24) are subordinate to the 3 main principles (pp. 19—21) and are valid only insofar as they do not contradict these. In some cases the differentiation of homonomous structures or the polymorphism of individuals is typical for a group but some of its members do not show these differentiations. This means that metamorphosis reverted secondarily to a state which has to be assumed as the starting point. An example is the uniform segmentation of the body of many insect larvae which has to be assumed for Arthropoda in general, but is not applicable to the special type of insects.

If none of the corresponding states of typically similar organisms can be considered to have morphological primacy, the mean value has to be considered as typical. This rule is not important for the determination of types, but it permits their visualization, determining body proportions and other numerical values which could not be determined otherwise.

e. ATYPICAL SIMILARITY

Systematic morphology deals with the variety of organic forms from the point of view of typical similarity, not general similarity. There are also atypical similarities or "convergences" which the morphologist has always found difficult to identify. It is characteristic for these similarities that during the arrangement of the similar structural elements into the respective wholes and during consideration of their development one finds that these similar structures are in contradiction to the systematic position of these forms. Atypical similarities must be eliminated in systematic morphology. The two types of similarity are traditionally known in comparative anatomy as "homology" and "analogy."* Atypical are similarities which approximate the later members of different systematic ontogenetic or paleontological sequences and thus reduce the contrast between the preceding, not or less similar members of these sequences. This is convergence of the series, instead of typical divergence.

Atypical similarities are common but do not form a coherent system of relationships which requires interpretation in principle. The existence of these similarities has resulted in the erroneous theory of "network relationships" (cf. also Naef, 1919, p. 54).

f. IDEALISTIC MORPHOLOGY AND PHYLOGENETICS

Darwin stated that it is not a scientific explanation to make an ideal
26 "plan" according to which related organisms are constructed. It cannot be denied that the theory of evolution and the phylogenetics based on it are closer in many respects to natural science than the concepts of idealistic morphology. On the other hand, the theory of evolution has developed from the study of ideal relationships and is based on the natural systematics which developed from this study, and it has to be assumed that each advance of idealistic morphology will result in an advance of the theory of evolution. It has not been proved so far that one can proceed logically in phylogenetical theory without recourse to idealistic morphology.

If the organic variety of forms is interpreted and classified in accordance with these views (or a part of it, as will be done for the dibranchiate cephalopods in the special part), it emerges as a system of idealistically interpreted relationships in the form of a genealogical tree (p. 12) which can be readily translated into phylogenetic terms. Phylogeny has achieved this and nothing else. To justify the basic concept that systematic relationships are in fact the expression of phylogenetic relationships, phylogeny has produced a series of circumstantial proofs by which the original hypothesis was consolidated into a theory (pp. 5—6).

Accordingly, the terminology of the earlier idealistic morphology was replaced with a new terminology suitable for the new concepts as follows:

Previous term	New term
Relationship of form	Blood relationships
Metamorphosis	Phylogenesis
Type	Ancestral form
Typical states	Primary states
Lower animals	Primitive animals, etc.

These changes, however, are not based on an essential revision of the idealistic morphology. Neither the specific results nor the basic concepts of idealistic morphology were subjected to a critical examination, which was especially necessary because of the revolution of concepts. From its beginning, phylogenetic morphology always moved in the dark, since the material reality in which the more subtle considerations of idealistic morphology resulted, caused the vague and esoteric principles of this science to be neglected or forgotten. Scientists believed to be dealing with facts, and ideas appeared superfluous.

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* But in a very imperfect manner, since the comparative anatomist is not interested in analogy. Furthermore, homologous parts are often also analogous. This approach does not go to the crux of the matter.

It was not realized that the search into the past from the point of view of historical morphology required a new methodological approach, different from that which had been used in the recognition of ideal relationships or the proof of the theory of evolution. It was particularly necessary to obtain historical evidence and to examine thoroughly the nature, value and reliability of the available facts. This has still not been done, and the need for a change in this field determined the character of the present work to a large degree.

Morphology is a historical science. Like any branch of history it has to
27 prove to what extent the past determines the present. Closer examination shows that it is impossible to understand the present state of organic beings without reference to their earlier states, especially with regard to structural relationships. On the other hand, the inclusion of such "early states" in the "explanation" provides a valuable insight which can reveal the rules which govern the conversion from one stage to the next. The historical view forgoes (nolens volens) the examination and determination of these rules and is restricted to assuming that a given state is conditioned in principle by the preceding states and to determining the series of former states.

Since every state of an organism is a variable system and can be directly associated only with its immediate precursor (and its energetic situation), earlier relationships can be traced only indirectly. It is an established fact that higher organisms have a history dating back to the mature egg which includes a series of increasingly complex stages, each of which is determined by its precursor. This "ontogeny," or individual "developmental history," is well known in a large number of cases.

We also know another type of history, the development of the egg cell itself which exerts a direct influence on the course and results of ontogenesis. We know, for example, that the ovum undergoes certain changes after fertilization, that earlier the ovum developed the so-called maturation phenomena while still in the maternal body or after leaving it, and that still earlier the ovum was formed together with others by a number of divisions developing from a primary ovum which in turn developed from a mature ovum. The ovum thus has a history of its own, having developed by a number of cell generations from an identical earlier ovum. This cyclical development, perpetually reverting to its starting point, may be termed "germline development."

We do not share the apparently resonable view that descendants are the product of the parent body. The germ cells are indeed harbored by the parent, but they do not take part in its biological activity. Historically, germ cells develop directly from earlier germ cells. The fact that ordinary cells in plants or lower animals assume (or retain) the function of germ cells and produce a new multicellular individual does not change the above rule in principle, since also in this case these cells were not produced by the parent organism but participated in the formation of the parent organism. The cells form the cell states, but these do not produce their cells.

The existence of a sharp contrast between the somatic and the germ cells in higher organisms, especially animals (Weismann's germ plasma theory)
28 only stresses this relationship but does not create it. Since we are dealing

here with the phylogenetics of higher animals, this contrast is a fact. Animals capable of regenerating an amputated limb repeatedly cannot regenerate a gonad, although the limb has a much more complex structure. This proves that germ cells have a development of their own and become active only during reproduction, like a root which begins to produce a new shoot.

The cyclical-rhythmical development of the germ line in higher organisms resembles the development of living cells generally, especially the Protozoa, the most primitive unicellular organisms. In this light the germ cells appear as the basic or primordial form of all organic development and as the precondition of the continued existence of life. In contrast to the cyclical-rhythmical development of the germ line, the development of higher animal and plant individuals which is based on it may be named "terminal": from its conception the organism is doomed to die after reaching a certain complex state of organization, generation after generation. During its flourishing, however, the organism continues the development of the germ line and protects it from adverse environmental factors.

The germ line (or more generally the development of the cell) is the true bearer of organic history which guarantees the continuation of life from one generation to another, while the higher organism dies after having fulfilled its function. This is the relationship between the endless development of the germ line and the ephemeral existence of the multicellular organism. Phylogeny, which we consider as the history of higher organisms, represents a continuous series of germ lines and not a succession of countless generations of plant or animal organisms, as is generally thought.

An interrupted history is no history at all. Phylogeny is a true history and cannot be represented as a line of ancestors, even if this were directly observed. The members of such a line of ancestors are not stages of a process; the evolution they simulate is only imaginary! Idealistic morphology was doubly justified in conceiving the connections between related forms as ideal, as these connections remain ideal also for us!

Let us return to our analogy. During the brief period of observation,
29 the "underground root" of the germ line produces only identical shoots. As the theory of evolution postulates, however, the root changes with time. This forces us to assume that the shoots which appear continuously from the advancing root change slowly but constantly from one generation to another. The individuals formed today by the same continuous germ line are no longer identical with those produced previously, and future individuals will differ from those existing at present. The historical course of phylogenesis can be visualized as a lineage, i. e. a series of successive forms. However, the ancestors do not merge directly with each other, but each dies while (and often before) the next develops and therefore cannot show the true nature of history. However, phylogeny can be represented by a true lineage if we consider each individual ancestor as the result of the state of the germ line at the moment the ancestor was formed. The lineage of ancestors thus becomes a function and symbol of phylogeny.

The organic forms we deal with thus have a twofold history: an individual history, or ontogenesis, and a tribal history, or phylogeny. With the above reservations (!), phylogeny can be regarded as the gradual change of the species along the line of ancestors.

Phylogenesis is unfortunately often understood as a line of developed individuals and this is an artificial and harmful restriction of the concept. It must not be forgotten that the existing form of a plant or animal is embodied in the whole typical evolution and not in the developed organism alone. This is especially true of higher animals, whose embryonic and larval development often shows a large variety of stages which later disappear. Omission of these stages in a phylogenetical study would result in false conclusions. To avoid such an artificial interpretation of the facts, phylogenetic development, i. e. the lineage, must be considered as a sequence of progressively changing ontogeneses.

This interpretation results in a revision of the "biogenetic law." If ontogenesis is a repetition of a something, this something can only be the ontogenesis of the ancestors, and if reminiscences of earlier conditions occur in ontogenesis, they should be interpreted and formulated differently from Haeckel, who assumed a direct "causal connection" between ontogenesis and phylogeny and considered ontogenesis as "nothing else" than a recapitulation of phylogeny (cf. Naef, 1917, 1919).

These views on the relationship between development of the germ line
30 and that of the individual are of interest also from another aspect. They eliminate the contrast between relationship and homonomy in typical similarity. "Consanguineous" individuals, whether living in succession or at the same time, appear as members of a single whole, branches of the same trunk, like the homonomous limbs of a crayfish. Both are really connected by the continuity of cellular development, and the "metamorphosis" or "variation" of both appears to be causally based on similar principles. This view is only briefly touched on here. I will discuss it later in connection with a general theory of morphogenesis.

Another basic concept of phylogenetics, phylogenetic relationship, needs closer examination. Consanguinity is often discussed in phylogenetics, as if its definition were beyond doubt. In fact there is great difference between the relationship among bred individuals, which can be expressed genealogically, and phylogenetic relationship. Both involve a steplike gradation. However, the gradation of the relationship within a family has nothing in common with that of phylogenetics, which is interpreted more simply. Application of exact genetics to phylogenetics may perhaps change this situation by providing, for example, a closer connection between species formation and the actual relationships between forms. At this stage, however, the phylogenetic relationship is interpreted as a tribal or species relationship, while the individual relationship is presumed to exist in each species, without being considered in detail (cf. p. 31).

In its substance, the theory of evolution abolishes the concept of species in its most general sense (pp. 11—12). Organisms which today belong to different species but developed from a common ancestor are actually a single species. The proponents (like myself) of the monophyletic origin of life believe that in the final analysis all living creatures evolved from a single species. However, at a given time or during a limited period there is always a certain number of communities of reproduction or species, if only the potentialities existing at that time are taken into account. The species concept will be applied further on in this sense. Because of the extremely slow pace of phylogenetic changes, the period does not have to be precisely determined — years, decades or centuries are but brief moments in the course of phylogeny, but in which species exist. (In the graphic representation of the genealogical tree, the species existing at a given time are represented by a cross section of the branches and the recent state by the end of the branches.)

This leads us to the concept of "phylogenetic series" (Stammreihe). In tracing the history of a recent species we must assume that its ancestors
31 always belonged to a single "species," to the beginning of life. At any period of history the "ancestral form" of a recent species is represented by a stage in its phylogenetic (or species) development. Of the infinite number of such stages we shall deal only with those required to illustrate the changes, as in ontogenesis. Such a succession of ancestral forms will be referred to as "phylogenetic series." This is quite different from the "lineage" of individual genealogy, although the two are often confused.* Phylogenetics has no connection with the clarification of the individual genealogy which in the case of dioecious reproduction can only be represented by a complex network, but only with the relationship between species (Hertwig, Werden der Organismen, II ed., 1918, p. 236).

The only relationship between different species is the presumed or proven existence of a common preceding state in the ancestral form. The criterion for such a relationship is the common ancestral species, like the common type in idealistic morphology. This gives a complete analogy to the relationships in monoecious reproduction. The genealogical tree thus becomes an adequate expression of phylogenetic relationship, but it cannot fully illustrate the blood relationship in dioecious reproduction. This proves that the criticism of the use of the genealogical tree in morphology on the grounds that it is taken from genealogy, only in which it is justified, is not correct.

The genealogical tree is the only adequate method of illustrating an assumed phylogenetic (or systematic) relationship. Any other representation involves numerous compromises and conventions; the same is true for the usual form of the natural system (p. 15).

g. PHYLOGENETIC EVIDENCE

Phylogenetic research is impossible without historical evidence. There is naturally no direct evidence of phylogenetic relationships, but the natural system, i. e. the sequence of typical relationships, may serve as an indirect expression of such relationships. This is also true of such unquestionably parallel phenomena as individual development and paleontological evidence. We have thus 3 types of evidence for phylogeny: ontogenetic, systematic and paleontological. The past of an organism can therefore be determined from the following facts:

a) the position in the natural system, and also the systematic steplike sequence which led to this position (p. 13);

32 b) the series of its ontogenetic stages, or the ontogenetic gradation from which it developed;

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* The following terms have to be compared and distinguished: "transitional series" (Uebergangsreihe) (pp.9–10); gradation (Stufenreihe) (p.13); lineage (Ahnenreihe) (p.29); phylogenetic series (Stammreihe).

c) the paleontological gradation, i. e. the geological age and the order of the geological occurrence of the systematic precursors. There are no other sources!

The last two series of phenomena have been partly evaluated by the idealistic-orientated systematic morphology. The natural system thus always contains the nucleus of what can be clearly formulated in any particular case. The three sources of information are, however, not applicable only as a historical interpretation of the three main principles of natural systematics (pp. 19—26), but also to individual cases. In fact, ontogenetic and paleontological data contain elements which permit a historical interpretation independently from the natural system. We shall therefore examine these three sources more closely.

a) **The systematic evidence**, based on the natural system and expressed as a genealogical tree, is based on the main principle of the theory of evolution which states that the degree of typical similarity is a measure, or a result, of the degree of phylogenetic relationship. Systematic steplike sequences, represented by series of ideal types, have to be considered as phylogenetic (i. e. tribal) series in which each type is the prototype of a group of species derived from it. Naturally, any gaps or uncertainties in the determination of the typical are reflected in our idea of what is primary phylogenetically. It has to be mentioned that systematics does not give complete phylogenetic series. The number of phylogenetic types to be ascertained, i. e. the methodically accessible types, depends on the existing variety of forms (p. 13); hence the limitations of our phylogenetical knowledge. (If Octopoda did not exist, nothing could be ascertained about a dibranchiate ancestor of Decapoda!)

b) **The paleontological evidence** is not simply the sum of observations on extinct species. Extinct animals have to be approached differently from existing species because our knowledge of them is incomplete.* This knowledge is often restricted to geological dating. Paleontology only tells phylogeneticists the time at which certain species, genera, families, etc. appeared and vanished (became extinct or changed into other forms), and such information should be treated with care. Only positive data are certain, while negative data, i. e. the absence of certain types in certain strata, are often due to insufficient knowledge of the extinct group. Only a small fraction of the large variety of extinct forms is available, even if organisms that could not be preserved are excluded.

33 Paleontology does not provide direct evidence for a line of descent. Continuous series of transitions have only been observed with certainty in a few cases in close proximity, but the discovery of such phylogenetic series is of more importance as a proof of the theory of evolution than as a specific method for determining the general relationships. Even complete paleontological information does not present the individual facts in their organic context (i. e. as lineages). The linkage of these facts into true phylogenetic sequences is generally hypothetical. From the phylogenetic aspect, paleontology is thus placed at a disadvantage with respect to ontogenetics, in which morphological relationships can be interpreted historically as natural and coherent connections.

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* A historical fact is not that something existed but the proof that something existing in the past was the preceding stage of a successor.

c) **The ontogenetic evidence** is demonstrated in the individual development of organisms. Since F. Müller and E. Haeckel, this process has been considered as a shortened recapitulation of phylogenesis. Idealistic morphology proved that the ontogenetic stages correspond to the systematic stages, more exactly to the homologous stages of the preceding systematic stages (p. 11). Translation of these systematic stages into phylogenetic stages requires a new formulation of these ontogenetic-phylogenetic relationships, as done by Haeckel rather more suggestively than precisely in his biogenetic law. Ontogeny is not a "repetition" of phylogeny since this (p. 28), whether symbolized as a lineage or genealogy (p. 29) or represented in its true form, is basically different from ontogeny.

Ontogenesis repeats the preceding ontogenesis of the ancestors which these phenomena resemble. According to phylogeny, however, there is a gradual divergence from one ontogenesis to the next. This divergence is such that the earlier stages of the ontogenesis are increasingly more conservative than the following stages (with some reservation: see p. 19). If this is a law, the observed morphological relationships should necessarily follow. The validity of this law is evident from the general causal connection throughout the development. I have attempted a more precise formulation of this law elsewhere (Naef, 1917, p. 57). We may therefore assume that every stage of individual development of an organic form must be more primitive than the following stage.

Thus, the structure of the different parts of a developing individual repeats similar structures which occur in homologous stages of the ancestors and appear in the same order as these in the lineage. This formulation describes the evidence of the so-called "biogenetic law" and expresses more adequately than this the implications of the true law outlined above. Ontogenesis must thus be considered a well established historical document,
34 but it also provides the key for its interpretation.

Although ontogenesis gives no direct information about the adult ancestors, it does aid indirectly. The transitional forms observed in ontogenesis must have been destined to become other final forms, and their fate must have been different from what is observed today. This is the more probable in view of the fact that the same transitional forms are present in a large variety of organisms. For example, entire embryos of higher vertebrates (man) strikingly resemble those of lower vertebrates (shark).

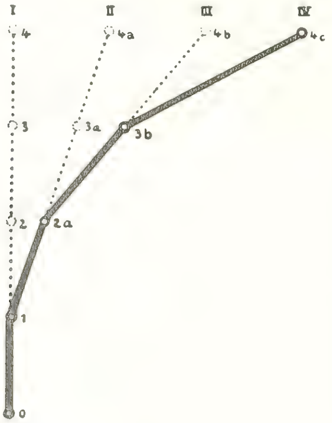

FIGURE 4. Ontogenesis (morphogenesis) as phylogenetic evidence. 0 – 4 are the stages of a morphogenesis with an indirect course. Each of these stages permits the construction of typical final states by direct development. This results in a series of transitional forms (I – III) which gradually leads to IV. If IV is a bird, III could be a reptile, II an amphibian and I a fish.

The transitional forms occurring are not equal in their apparent propensity to assume their different course of development, which is direct in some cases and indirect in others. Direct development involves complication and functional development of the parts without affecting the general plan, while indirect development involves changes of the primary topography and proportions, as well as a differentiation and division of function between originally equal structural elements. We consider the forms with direct development as the original forms, or in idealistic terms (p. 20) as typical; those with an indirect development are phylogenetically secondarily changed. Thus, indirect ontogenesis gives at least a suggestion about the structure of the ancestors of the given organism (Figure 4).

The sequence of stages of morphogenesis indicates a true lineage in which the respective "anlage" states developed once directly in the ancestors, while they developed further changes in their descendants.
35 However, ontogenesis is not a direct repetition of final stages of the ancestors; there is no palingenesis, in the sense of F. Müller and Haeckel, and therefore no cenogenesis either.

Individual ontogenesis can be considered as phylogenetic evidence quite independently of the fact that the comparison of ontogeneses is very important in natural systematics in which it assumes historical significance as well (pp. 19—21). The advantage of this phylogenetic evidence is that ontogenesis clearly shows the steps of a necessary natural connection between the stages, while paleontology and systematics only suggest such a connection, but do not contain it as tangible facts. Correctly interpreted, ontogenesis gives the most reliable information on the special phylogeny of a given form. However, the scope of this information varies from one case to another and is limited in direct development, in which the early stages follow the later stages in their change. One of two closely related forms may still show a phylogenetic reminiscence which is absent in the other (Naef, 1917, p. 60). F. Müller (loc. cit., p. 7) speaks correctly of an obliteration of the evidence. There is, however, no falsification of the evidence.

If we discussed above phylogenetic evidence separately from systematics, this does not mean a genealogical treelike relationship which is not contained in the idealistically orientated natural system. The whole realm of known facts and the relationships between them have already been exhaustively studied by the idealistic methodics, and phylogenetics could have restricted itself to translating and interpreting the results obtained by idealistic morphology. A phylogenetic evaluation of ontogenetic and paleontological data is nevertheless possible without discussion of the systematic-morphological relationships and even beyond them (Naef, 1919, p. 62).

Can the graded similarities be interpreted as direct historical evidence, as phylogeneticists have often done? The answer cannot be negative in principle. However, recent knowledge does not permit the use of similarities as evidence for blood relationship (pp. 6, 22, 26). I have chosen a logically irreproachable way in elaborating first the principles of the well tested idealistic systematic morphology for consistent practical use. Given such a solid foundation (a theory, no longer a mere hypothesis, see p. 32), phylogenetics can be applied to specific systematic-morphological tasks, as in this book, without taking up the controversial question of the course and causation of species formation. The following part describes the uncertainty which still persists in phylogenetics.

36 h. GENERAL PRINCIPLES OF PHYLOGENETIC VARIATION

Phylogeneticists often have the tendency to consider the whole change of organic life as progress, i. e. as a continuous, only occasionally interrupted rise from a dark abyss to ever greater organic perfection. Darwin's theory of the survival of the fittest in the struggle for survival has advanced this view considerably. There is no doubt that many steplike series show a progressive increase in size, strength, complication and variety. But this is not always true, since the opposite, i. e. progressive reduction and simplification, often takes place. I hope to be able to show that cases of such retrogressive development are much more frequent than progressive cases. This may seem paradoxical since geology shows a continuous progress of organic life.*

Progress which affects only a few lines already appears as a striking phenomenon, which may mask all other trends. Thus, the retrogressive characters recede into the background despite their greater frequency. An innovation like the modification of some of the suckers of decapods into hooks, has to occur only once (in an ancestral species) and may have disappeared frequently during or after the formation of new species (Chapter 3). It must be borne in mind that our methodics does not permit us to trace the change of species, but only to determine the systematic and phylogenetic stages (pp.13 and 32) at which the respective groups of forms diverged. Progress provides new possibilities which may become starting points for new, even if rare, variation. Many, perhaps all, phylogenetic stages will therefore correspond to forms which are particularly progressive in some respect. Progress in these stages means the appearance of new variety, but not necessarily a change of species.

Darwin's principle naturally does not mean survival of the most progressive forms in our sense, but the survival of the best adapted to an existing or new environment, possibly the smallest, most wretched and humblest form. This is an ecological, not a morphological principle.

Morphological progress is often parallel to ecological progress. The two courses have multiplication and differentiation in common. Multiplication means ecological strength and security. It is associated with the
37 cells, the ultimate known units of life. Cell division is a prerequisite for all progress. It results in multiplication of individuals and their parts, and thus provides material in which differentiation can occur.

Differentiation means at first only the appearance of a new form. But, as each form is an "apparatus", it also means a new function and if this proves true, a division of labor. All differentiations dealt with in systematic morphology have this ecological character. In this sense, "progress" can be defined as a frequently occurring course of development which is not unique but has its opposite and consequently cannot serve as a starting point for methodical investigation.

i. PRINCIPLES

1. Idealistic morphology was not only the precondition for the introduction of phylogenetics in the history of science, but has to be given priority

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* Progress is interpreted here only as complication and an increase of the degree of variety.

over it on logical grounds even today by creating the "natural system" of organisms (we cannot investigate things that do not exist any more; see pp. 6, 22, 26).

2. We consider the theory of "typical similarities" as the methodological foundation of idealistic morphology. Typical similarity is the similarity between complex units which consist of similar parts in the same arrangement (pp. 8—11).

3. Typical similarity exists between organisms in general, especially with regard to their forms, functions and adaptations. Systematic morphology is the study of organisms in terms of typically similar forms (pp. 7—8).

4. Typical similarity is analogous to geometrical similarity, particularly in the sense that each part of a structure is "homologous" or "corresponds" to some part of another structure. Typical similarity is thus an ideal relationship between forms, which is expressed in the homology of their parts. In the final analysis, however, typical similarity exists not between fixed but between developing forms, i. e. between entire ontogeneses to which these forms belong (pp. 8—11).

5. The type is primarily a "tertium comparationis" in the comparison of typically similar single forms, and relates a multitude of such forms to an ideal center. The type appears as an expression of objective necessities in this application. The relationship between individual forms and the type is comparable to that between individual cases and the law (Goethe).

6. The typical is determined by comparison of the individual parts with observance of a "morphological primacy" of certain parts or characters. This is done according to certain principles (p. 18).

7. There are 3 main principles of morphological primacy: ontogenetic, paleontological and systematic precedence. All three develop historically-
38 dynamically from the primacy of cause over effect (p. 22), but they can also be derived directly from the morphological relationship of the forms observed and thus be based on idealistic morphology (pp. 19—22).

8. The primacy of ontogenetic precedence means that in the course of a morphogenesis, an earlier stage is more important in the determination of the typical than a later stage which developed from it. This is a more precise and restricted formulation of the so-called "biogenetic law" and the old theory of the parallel between ontogeny and the "animal series." Earlier stages are to be considered as more important only insofar as they are the cause of the following stages (pp. 19—21).

9. The primacy of paleontological precedence means that among the corresponding states of typically similar organisms, those which are more important in the determination of the typical are the ones which occur in earlier geological periods. This can be based on the fact which is proved by comparison based on other principles that such forms are closer to the type (p. 21).

10. The primacy of systematic precedence means that among the corresponding states of typically similar organisms, those which are more important in the determination of the typical are the ones which occur in the preceding systematic rank, i. e. those which are typical for this category. This follows from the logical nature of the systematic sequences. These proceed from larger to smaller categories and what is valid in the larger unit must also be applied in the smaller unit (p. 19).

11. Embryological facts provide the most reliable information on the typical and its relationship to the "derived". There is in ontogeny a gradual transition from certain basic or primary forms to a variety of derived states (p. 21).

12. From these considerations emerges the concept of metamorphosis, in which observed (and ideal) individual forms (including adult forms) are arranged theoretically in a series, like the stages of a process. Metamorphosis is the ideal combination of typically similar forms by transitional stages (transition series) (pp. 9—10).

13. By such a process, i. e. by a series of transitional stages, the individual forms appear to be connected with their type. The type is then the abstract (but naturally possible) individual form from which a multitude of typically similar forms can be "derived" by the most simple and naturally possible metamorphoses (p. 10).

14. Typical similarity is the foundation of the natural system since it places the forms (species) related to one type in a single systematic category. If such types are again typically similar to each other, the first formed categories are united in a higher category with a higher type (p. 12).

39 15. The relation between coordinated and subordinated categories is best represented graphically in a "genealogical tree," which does not necessarily reflect phylogenetic relationships. Such a genealogical tree shows most clearly the state of abstract coordination and subordination (systematic sequence; pp. 12—13).

16. Systematic categories can usually be characterized by mere definitions ("diagnoses"). However, these definitions have less practical value than the types. A major disadvantage of diagnoses is that they do not show the correlation, i. e. the indisputable connection of characters or parts with the natural whole (pp. 13—15).

17. According to the theory of evolution, typical similarity of species (or relationship of forms) results from their phylogenetic relationship (blood relationship) (p. 26). It is therefore justified to transfer the relationships established by idealistic morphology into a historical frame in which the morphological characters of the ideal type are identical with those of a real ancestral form. Phylogenetic morphology can thus be established on the basis of idealistic morphology.

18. Like all true natural science, phylogenetics attempts to explain or reveal the causes of organic morphogenesis. This attempt is, however, restricted to the historical aspect, i. e. the determination of the early states from which a certain form has developed and to which it can be traced back (p. 27).

19. Phylogenetics is thus intimately related to ontogenetics, which describes the directly preceding stages of the given forms and traces them back to the mature egg. Phylogeny can thus be defined as the prehistory of the egg and it culminates in the analysis of the germ line, which ensures continuity of life and form. Phylogeny deals thus with the changes of the hereditary mass during the development of the germ line (pp. 27—29).

20. Phylogeny cannot be represented as a lineage or a sequence of ancestors since these ancestors are not stages of a process and are only indirectly related. An evolution which apparently exists in this process is only abstract (in the sense of idealistic morphology, to which we always have to return) (p. 29).

21. Phylogenetics cannot produce a new concept of homology either. If we relate the various structures to corresponding parts of an "ancestral" form, we merely state that these structures are homologous to their ancestral counterpart, i. e. we take the concept of homology for granted. Neither can embryology produce a new concept of homology (pp. 8, 20, 28).

22. Lineages of ancestors can nevertheless symbolize phylogeny, since the structure of the ancestors can be considered the result of the condition at which the germ line had arrived at the moment of its appearance (p. 27). Even in this sense, however, the lineages represent only sequences of developing organisms, i. e. successive ontogeneses.

40 23. With this interpretation, ontogenesis cannot be a repetition of phylogeny, as the so-called "biogenetic law" maintains; this applies also to cenogenesis, etc. There is no palingenesis in the sense of E. Haeckel, in which the adult ancestral stages are repeated in some fashion (pp. 33—34).

24. The structures observed in some parts of the developing individual repeat similar, homologous structures which existed in homologous stages of the ancestors. These structures appear during the transformation of these parts in the same order as they did in the lineage (p. 33).

25. The special significance of paleontology for phylogenetics consists in the fact that paleontology can date fossil forms which have to be treated like the recent forms. The disadvantage of paleontology is that it does not present the natural connection between the facts, which embryology does. All sequences between fossils have to be constructed (pp. 32—33).

26. Phylogenetics abolishes the species concept in its old, generalized sense. Species are only communities of reproduction which exist for a limited period. The majority of such species are "phylogenetically related" (hypothetically) in the sense that they have developed from a common ancestral species (p. 30).

41 3. THE FORM OF SYSTEMATIC-MORPHOLOGICAL PRESENTATION

We shall not discuss the application of the above principles in systematic-morphological research for various reasons. However, their significance in the presentation of results will be considered. In the preceding part we attempted to explain the abstract meaning of certain formulations and terminologies which are widely but inconsistently used. It is evident from the above that an ideal relationship of typical similarity must be the leading factor of a systematic work, while the mere individual facts can provide the material but not the organizing meaning of such a study. A treatment based on graded morphological relationships, like types in a genealogical tree, is a more coherent whole, superior to a mere collection of data. Such a concept places each fact in its proper place which clearly reflects the degree of its generality or its special characters. Variety thus becomes a unit, and factual knowledge becomes an insight.

Such a representation is only possible if there is thorough factual knowledge as well as completeness of morphological abstraction. Doubts and gaps in our knowledge will persist but a certain completeness within the existing possibilities can and must be achieved. This is a laborious, time-consuming endeavor, ill suited to all the other urgent tasks before me.

The presentation must be deductive, proceeding consistently from the general to the particular and following the stages of the natural system to species, and it must show the latter as particular metamorphoses of the generic type. Although this approach is self-explanatory and natural, it has not always been consistently followed, and even in this book we have applied it only to a certain extent. A certain uneveness of presentation could not be avoided. Such deviations will be indicated in the text, for having criticized the lack of principles in others, the author would not like to see his own principles associated with a faulty presentation.

42 The chapters of the following main part describe systematically ideal and concrete species with similar morphology. If the systematic units of each order are based on ideal types (p. 12), they must be described according to these types. Each main chapter therefore contains a description of a species as the type of a genus, family or order.

The description of each type is preceded by a diagnosis of the respective systematic category, first, to serve a practical need and second, to give a brief summary of what is found constantly and generally in the whole group. All characters mentioned in the diagnosis are omitted in the discussion. This facilitates the description of the type, since a general character is necessarily also typical. The diagnoses therefore contain important information on the determination of the type and reduce to some extent the problematic image to which the type is naturally prone. The preceding diagnosis makes many stereotypic considerations unnecessary and introduces a strengthening element in the structure of a systematic-morphological presentation.

For the sake of clarity, adult forms described in the larger and general chapters are treated separately and before the transitional postembryonic stages. A division into many special chapters would have been chosen if the factual material had been of ideal completeness and had permitted morphological abstraction. We would have then attempted to proceed from the youngest to the oldest stages and would have placed one ontogeny next to another, regardless whether the particular development is typical (ideal), hypothetical (inferred)* or actually exists.

However, separate treatment of the adult forms has its advantages. Heterochronisms of development are of less systematic interest. The manner in which typical details emerge is always the same, and morphological variety reaches its peak in the latest stages. Hence the dominating importance of the description of the adult stages. Data on ontogeny only constitute a natural addition to the description of the final state, presenting it as the result of an accomplished process.

The description of the typical is followed by a discussion of the "metamorphosis" or "variation" of the type in the respective group. This approach stresses the inner coherence of the system by describing not only the unity of form but also its variation. Auxiliary ecological considerations explain metamorphosis as a process of adaptation.

43 The terminology used is mainly that of idealistic morphology, but it can be readily translated into historical terms according to the above principles. Indifferent (ambiguous) terms are also frequently used. An example is "prototype" (Urform), which can mean either "type" (ideal form, Typus) or "ancestral form" (Stammform). Description of typical similarities is always stressed; a strictly historical presentation was used only in cases in which extensive use of paleontological data was attempted or was possible and in which the metamorphosis had to be orientated in time.**

Clarity is a general demand. Pictorial presentation of the observed forms is doubtless worth far more than long descriptions in a systematic morphological work. We used therefore a drawing technique which permits the publication of a large number of drawings at relatively low cost. The specialist will find that the figures form a major, perhaps the most valuable, part of the work. They are drawn after carefully selected individual preparations or living specimens as far as their measurements and proportions are concerned, not only reproductions of objects. Inessential and accidental details are omitted. The typical in their outline, symmetrical proportions, etc. have been stressed, often at the expense of the artistic effect.

However, also ideal concepts, obtained by morphological abstraction, had to be presented insofar as they referred to relations of form. Their omission would have meant that the ideal concepts have no practical value and have no place in a scientific work and that one should cease to speak of prototypes and ancestral forms and their properties. But if these structures are useful auxiliary tools of methodical morphology and systematics, they deserve appropriate treatment. To save space and labor, only types of major groups have been drawn; for the smaller categories the reader is referred to figures in which individual typical characters are illustrated.

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* The actual existence of which in the past is assumed or maintained.

** On the historical interpretation of the ideal relationships and the "genealogization of the system" see concluding sections 1 and 2 of this volume, as well as my article "Palaeobiologie und Phylogenetik" in Abh. theor. Biol., Schaxel, Berlin. 1920.

44 4. PRELIMINARY SYSTEMATIC-MORPHOLOGICAL ORIENTATION

Contents: a. Definition, position and division of the class (historical). b. Systematic review of the main groups. c. Systematic review of families and genera. d. Scheme of the organization of molluscs. e. Normal orientation of the body.

a. DEFINITION, POSITION AND DIVISION OF THE CLASS

Aristotle, who had an astonishing knowledge of Cephalopoda, placed them in the class "Malakia" and always treated them separately. Linnaeus took a step backward by placing the Cephalopoda partly in the "Vermes Testacea" and partly in the "Vermes Mollusca." The Cephalopoda were again united by Schneider (1784). Cuvier gave the class its present name, which became generally accepted (1798). However, he placed also the fossil Bellerophontidae as well as the Foraminifera in the class. Blainville (1825) recognized the Bellerophontidae as Gastropoda, while Dujardin (1835) transferred the Foraminifera to the Protozoa. The definition of the class has since remained unchanged, except for an attempt by Lankster (1885) to include the Pteropoda.

Cephalopods are generally considered as the most highly developed branch of molluscs. This is true in terms of morphological complexity and variety; the question is whether there is a special relationship with one or several other classes, and whether the organization of Cephalopoda can be derived from a "lower class." Such attempts have been made, of which only two will be mentioned. Grobben (1886) considered Dentalium as a starting point, and Simroth (1905) the snails. Both attempts are based on vague similarities of certain details and are fantastic, without determining the typical general organization of both groups and without methodical comparison.

I shall not enter into a detailed discussion of the relationships between the major groups of molluscs; a work on this subject will be published elsewhere. My long experience with molluscs has shown that the recent forms can be divided into 6 clearly defined and equivalent types, none of which can be derived from another of these groups. These are the Cephalopoda, Gastropoda, Lamellibranchiata, Scaphopoda, Placophora and Solenogastres.
45 The relationships among these 6 classes, to which I add the fossil Odontomorpha (including Hyolitha, Tentaculita and Conularida) cannot be based on a reconstructed primary type, but only on a more indirect connection because each class shows definite typical similarities with at least one other class. No generally valid diagnosis can be given.

Critical analysis of the data provides facts which cast doubt on the prejudiced concepts of the primary organization of molluscs. Based on some species of Gastropoda and Chiton, these theories consider the Patella type as the primary form of molluscs. It was shown long ago, however (cf. Naef, 1911), that all Patella-like snails evolved from species with a normal spiral shell and are not related to any primary form of snails. Chiton, on the other hand, is far too problematic in its entire organization, particularly the structure of the shell, which determines the habitus, for any conclusions to be based on it. The accepted theories are therefore without foundation.

Some closer relations certainly exist among the six recent classes of molluscs. Solenogastres and Placophora differ sharply from the other classes. This has led to the division into Amphineura and Eumalakia (Naef, 1911), the mutual relationship of which is very problematic. This is a great difficulty for a general orientation of the morphology of molluscs. However, the Cephalopoda form a more closely related systematic unit with the Gastropoda, Lamellibranchiata and Scaphopoda, in which the Cephalopoda and Gastropoda are most closely related. The Cephalopoda provide a connection between the above four classes on one hand and Chiton and the Amphineura on the other.

The relationship between molluscs and other Metazoa is still very debatable, but it appears* that molluscs originated from the Annelida. This view is based on basic and indisputable similarities in the embryology of the two groups (see Naef, 1913).

The general division of the class has already been determined in general, and I hope to be able to complete it. Aristotle correctly distinguished between the Octopoda and Decapoda, and this was revived by Leach (1817). Owen (1836) established the Tetrabranchiata and Dibranchiata as two opposite groups, and this resulted in the recent classification of the Cephalopoda. Reinhardt and Prosch (1844) introduced the Pteroti and Apteri as suborders of the Octopoda; Orbigny (1845) proposed the suborders Myopsida and Oegopsida for the Decapoda. This division is omitted here as artificial,
46 while the classification of the Octopoda is retained in its content, but in a new and expanded form (Palaeoctopoda, Cirroteuthoidea and Polypodoidea). Other classifications are those of Hoyle (1886: Lioglossa and Trachyglossa) and Grimpe (1917: Cirrata and Incirrata)(see chapter on Octopoda on these groups).

The division of the class is based on the historical development outlined above. A new element is the classification of the Decapoda into Belemnoidea (belemnite-like), Teuthoidea (calmar-like) and Sepioidea (sepia-like). This classification will be discussed in greater detail in the main section. The Oegopsida are retained as a subdivision of the Teuthoidea, whereas the "Myopsida" are abolished.

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* See the article of K. Heider on invertebrate phylogeny in "Kultur der Gegenwart," Part 3, Section 4, Volume 4. Abstammungslehre, pp. 504—511.

b. SYSTEMATIC REVIEW OF THE MAIN GROUPS

Class **CEPHALOPODA** Cuvier, 1798

Subclass I. Tetrabranchiata Owen, 1836
Subclass II. Dibranchiata Owen, 1836

Order A. **Decapoda** Leach, 1818

Suborder 1. Belemnoidea (Zittel) Naef, 1912
Suborder 2. Teuthoidea Naef, 1916
Suborder 3. Sepioidea Naef, 1916

Order B. **Octopoda** Leach, 1818

Suborder 1. Palaeoctopoda nov.
Suborder 2. Cirroteuthoidea nov.
Suborder 3. Polypodoidea nov.

c. SYSTEMATIC REVIEW OF THE FAMILIES AND GENERA OF DIBRANCHIATA

Order I. **DECAPODA** Leach, 1818

Suborder 1. **Belemnoidea†** (Zittel) Naef, 1912

Family 1. Aulacoceratidae nov.
Aulacoceras Hauer
Asteroconites Teller
Dictyonites Mojs.
Calliconites Gemm.
Atractites Gümb.
Family 2. Phragmoteuthidae nov.
Phragmoteuthis Mojs.
47 Family 3. Belemnitidae Blainv.
Belemnites Lister
Ostracoteuthis Zittel
Neohibolites Strolley
Bayanoteuthis M.-Chalmas.
Styracoteuthis Crick
Acroteuthis Stolley
Oxyteuthis Stolley
Macroteuthis Abel, etc.
Family 4. Belemnoteuthidae Zitt.
Belemnoteuthis Pearce
Diploconus Zitt.
Conoteuthis Orb. (?)

Family 5. Xiphoteuthidae nov.
    Xiphoteuthis Huxley
Family 6. Vasseuriidae nov.
    Vasseuria M.-Chalmas[*]

Suborder 2. TEUTHOIDEA Naef, 1916

a. **Prototeuthoidea** nov. †

Family 1. Belopeltidae Naef[**]
    Belopeltis Voltz (for "Loligo" aalensis = bollensis Zieten = "Geoteuthis" bollensis Münst.
Family 2. Geoteuthidae Naef
    Geoteuthis ("Belopeltis") simplex (Voltz) = G. lata = G. orbignyana Münst.
Family 3, Leptoteuthidae nov.
    Leptoteuthis H. v. M.
Family 4. Plesioteuthidae
    Plesioteuthis Wagn., Paraplesioteuthis Naef (for "Geotheuthis" sagittata Munst., see p. 143)

b. **Mesoteuthoidea** nov. †

Family 1. Trachyteuthidae nov.
    Trachyteuthis H. v. M.
    Glyphiteuthis Reuss
Family 2. Beloteuthidae nov.
    Beloteuthis Münst., Phylloteuthis Meek and Hayden (uncertain)
    Ptiloteuthis Gabb. (uncertain)
Family 3. Teuthopsidae nov.
    Teuthopsis Deslongchamps[‡] (not Teuthopsis Wagner)
Family 4. Kelaenidae nov.
    Kelaeno Münst. (This peculiar form differs markedly from the typical condition of this group.) The characteristic displacement of the cone to the dorsal

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[*] Contrary to the view of Leriche (1906) and Abel (1916), this genus is distinct from Belosepiella Alessandri. Belosepiella lacks a phragmocone and has only a Beloptera-like sheath. In Vasseuria, on the other hand, the sheath contains an alveole and is distinctly of the belemnoid type.

[**] The family, originally named Belemnosepiidae, also included Belemnosepia Buckl., Palaeosepia Theodori, Lolignites Quenst. and Sepialites Münst. These genera probably belong to Geoteuthidae Naef.

[‡] "Teuthopsis" Wagner is not "Teudopsis" Deslongchamps. This name was originally used for T. agassizi, which was later renamed Loliginites coriaceus Quenst. (Figure 61d); it was later applied to a form closely related to Beloteuthis bollensis (Zieten, Table 37), both from the Lias. For "Teuthopsis" Wagner I propose the name Palaeololigo and the Family Palaeololiginidae (see p. 145).

surface creates a modification of the mantle sac as in Opisthoteuthis[*])

c. **Metateuthoidea** nov.

a) Metateuthoidea myopsida (Orb., 1845) nov.

Family 1. Loliginidae Orb., 1845
Loligo Lam., Sepioteuthis Blainv. Alloteuthis nov., Loliolus Strp.
48 Doryteuthis Naef
Family 2. Promachoteuthidae Naef, 1912
Promachoteuthis Hoyle
Family 3. Lepidoteuthidae Naef, 1912
Lepidoteuthis Joubin[**]

b) Metateuthoidea oegopsida (Orb., 1845) nov.

Family 1. Gonatidae Hoyle, 1886 (as subfamily)
Gonatus Gray
Family 2. Benthoteuthidae Pfeff., 1900
Benthoteuthis Verrill
Ctenopteryx Appellöf
Family 3. Enoploteuthidae Chun, 1910
Pyroteuthis Hoyle, Pterygioteuthis Fischer, Lycoteuthis Pfeff., Lampadioteuthis Berry, Nematolampas Berry, Enoploteuthis Fér. and Orb., Abralia Gray, Abraliopsis Joubin, Ancistrochirus Gray, Thelidioteuthis Pfeff.
Family 4. Onychoteuthidae Gray, 1849
Onychoteuthis Lichtenst., Ancistroteuthis Gray, Teleoteuthis Verr., Chaunoteuthis Appellöf, Tetronychoteuthis Pfeff., Moroteuthis Verr.
Family 5. Neoteuthidae nov.
Neoteuthis nov.[†]
Family 6. Octopodoteuthidae Berry, 1912
Octopodoteuthis Rupp.
Cucioteuthis Strp.

[*] Kelaeno has no hooks. Hooks have not been found in any fossil teuthoid. My erroneous view was based on incorrect data of Münster, Meyer and Wagner, which appeared all the more credible as they were confirmed by J.Walther in 1905. The error is based on a faulty determination: the corresponding plate of Daiting with the cone, proostracum, head impression, eyes and arms in the Munich study collection does not belong here (contrary to appearances) but to Acanthoteuthis (p.112). This error has led to my view (pp.127 – 133) that the Teuthoidea and Belemnoidea evolved from a common ancestor with hooks. The hooks of Belemnoidea are not related to those of the recent Teuthoidea, although both have developed in a similar manner.

[**] This may be a special type of metateuthoid; in any case, it appears from the structure of the heart that it is not an oegopsid (cf. Chapter 4).

[†] Here also belong an undescribed species of oegopsid of which I have 3 young stages with the following description: habitus Sepioteuthis-like; fins lateral, rounded; mantle sac slender; gladius with sharp posterior cone, otherwise Loligo-like; arms short, biserial; clubs quadriserial.

Family 7. Histioteuthidae Verr., 1881
Histioteuthis Orb., Calliteuthis Verr., Meleagroteuthis Pfeff.

Family 8. Architeuthidae Pfeff., 1900
Architeuthis Strp.

Family 9. Brachioteuthidae Pfeff., 1900
Brachioteuthis Verr.

Family 10. Chiroteuthidae Gray, 1849
Chiroteuthis Orb., Mastigoteuthis Verr., Idioteuthis Sasaki, Joubinioteuthis Berry, 1920

Family 11. Grimalditeuthidae Pfeff., 1900
Grimalditeuthis Joubin

49 Family 12. Cranchiidae Gray, 1849
Cranchia Leach, Pyrgopsis Rochebr., Liocranchia Pfeff., Liguriella Issel, Phasmatopsis Rochebr., Toxeuma Chun, Taonius Strp., Desmoteuthis Verr., Megalocranchia Pfeff., Taonidium Pfeff., Cristalloteuthis Chun, Phasmatoteuthis Pfeff., Galiteuthis Joubin, Corynomma Chun, Teuthowenia Chun, Bathothauma Chun, Verrillioteuthis Berry, 1916, Leucocranchia Joubin, 1912

Family 13. Ommatostrephidae (Gill, 1871) Strp.
Illex Strp., Todaropsis Girard, Notodarus Pfeff., Ommatostrephis Orb., Dosidicus Strp., Hyaloteuthis Gray, Stenoteuthis Verr., Symplectoteuthis Pfeff., Eucleoteuthis Berry

Family 14. Thysanoteuthidae Keferstein, 1866
Thysanoteuthis Troschel

Suborder 3. **Sepioidea** Naef, 1916*

Family 1. Belemnosidae Naef
Belemnosis (differs from Spirulirostra)

Family 2. Belopteridae Naef
Belopterina M.-Chalmas, Beloptera Blainv., Belopteridium Naef (for Beloptera edwardsi Deshayes, 1825), Belopterella Naef (for Beloptera cylindrica von Koenen)

Family 3. Belospiellidae Naef
Belosepiella Aless.

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* Protosepiodea and Metasepiodea have been omitted, since transitional forms have been found.

Family 4. Spirulirostridae Naef*†
Spirulirostra Orb., Spirulirostrella Naef (for Spirulirostra szainochae Wojcik, 1903)
Family 5. Spirulirostrinidae Naef
Spirulirostrina (transitional to Sepiidae)
Family 6. Sepiidae Orb., 1845
Sepia L., Sepiella Strp., Hemisepius Strp., Metasepia Hoyle, Belosepia† Voltz
Family 7. Spirulidae Owen, 1848
Spirula Lam.
Family 8. Idiosepiidae Appellöf, 1898
Idiosepius Strp.
Family 9. Sepiolidae Tryon, 1879
Sepiadarium Strp., Sepioloidea Orb., Rossia Owen, Semirossia Strp., Heteroteuthis Gray, Nectoteuthis Verr., Iridoteuthis Naef, Stoloteuthis Verr., Sepiolina Naef, Euprymna Strp., Sepiola Leach, Sepietta Naef, Rondeletia Naef**

50 Order II. **OCTOPODA** Leach, 1818

Suborder 1. **Palaeoctopoda** nov. †

Family 1. Palaeoctopodidae Dollo, 1912
Palaeoctopus Woodward, 1896

Suborder 2. **Cirroteuthoidea** Berry, 1920, nom. nov.
(Pteroti Reinh. and Prosch 1846;
Lioglossa Lütken, 1882; Cirrata Grimpe, 1916)

Family 1. Cirroteuthidae Keferstein, 1866
Cirroteuthis Eschricht, Stauroteuthis Verr., Frockenia Hoyle, Cirrothauma Chun, Chunioteuthis Grimpe
Family 2. Opisthoteuthidae Verrill, 1896
Opisthoteuthis Verr., 1883
Family 3. Vampyroteuthidae Thiele, 1915
Vampyroteuthis Chun, Melanoteuthis Joubin, Laetmoteuthis Berry, Hymenoteuthis Thiele

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* Belemnosis Edwards, originally placed in this family, is stated by F. A. Bather to be probably an eroded Spirulirostra. I accept this view in the sense that I consider the abberrant shell fragment to belong to a Spirulirostra-like form (Bullen-Harris, 1894).

** The name Rondeletia Naef, 1916 is already occupied by a fish and should be changed to Rondeletiola (Proc. U.S. Nat. Mus., Vol.17, p.454).

Suborder 3. **Polypodeidea** nov.
(Apteri Reinh. and Prosch, 1846; Trachyglossa Lütken, 1882; Incirrata Grimpe, 1916)

a. Ctenoglossa nov.

Family 1. Amphitretidae Hoyle, 1886
Amphitretus Hoyle
Family 2. Bolitaenidae Chun, 1911
Bolitaena Strp., Eledonella Verr., Vitreledonella (?)

b. Heteroglossa nov.

Family 1. Octopodidae Orb., 1845
Octopus Lam., Scaeurgus Trosch., Eledone Leach, Velodona Chun, Cistopus Gray, Pinnoctopus Orb., Graneledone (Joubin, 1918)

Family 2. Argonautidae Cantraine, 1841
Argonauta L., Ocythoë Rafinesque, Tremoctopus Delle Chiaje, Alloposus Verr.

51 d. SCHEME OF THE ORGANIZATION OF MOLLUSCA

A detailed treatment of the original structure or typical organization of molluscs involves a discussion of a large number of data and is beyond the scope of this work. However, a general outline of the phylum Mollusca will be given. For didactical purposes, this will be based on a scheme which describes a number of morphological aspects without pretending to be a reconstruction of the ancestral form or of a methodically constructed type.

This scheme represents the relationships in the subclass Eumalakia (Naef, 1911) (Cephalopoda, Gastropoda, Lamellibranchiata and Scaphopoda)
52 more accurately than those in the Amphineura (Placophora, Solenogastres). It shows an undivided, strictly postvelar shell (21), of which the conical shell has to be considered as the primitive form. Such a shell permits a gradual change from a flat or blunt form to various degrees of a pointed, long form with corresponding changes in the scheme. The apex of the shell (22) represents the primordial or embryonic shell, the origin of which will not be discussed here. The later form of the shell is the result of more or less uniform marginal growth by continued deposition of fresh shell substance on the free margin of the shell. This growth is evident in the growth lines of all typical shells of molluscs, in which the successive stages of development can be followed. The solidity of older shells, however, depends on growth in thickness, i. e., secondary deposition of new shell structure on the inside of the original plate. It produces a thick, lamellar strengthening layer (hypostracum or nacreous layer). The nonlamellar substance produced by

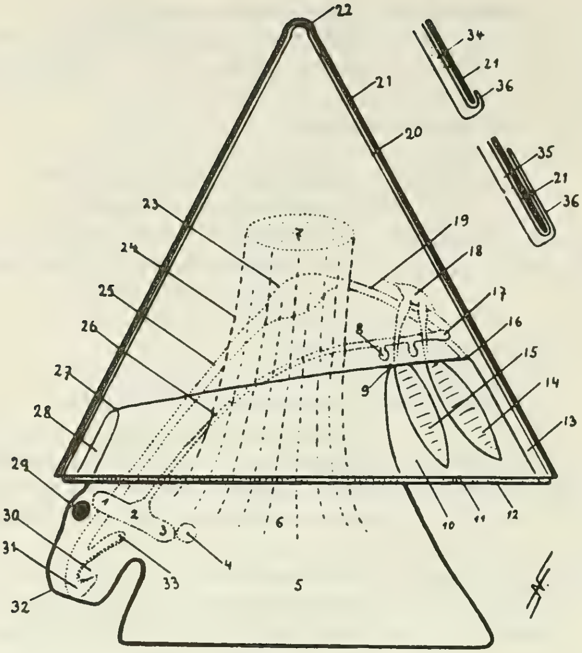

FIGURE 5. Scheme of organization of molluscs:

1 — cerebral part; 2 — pleural part; 3 — pedal part of the esophageal ring; 4 — statocyst; 5 — foot; 6 — projections of the retractor of the cephalopodium or shell adductor; 7 — insertion of this muscle on the shell; 8 — anterior branchial ganglion; 9 — median point on the anterior transverse mantle groove; 10 — posterior part of mantle cavity; 11 — free margin of shell; 12 — free margin of mantle; 13 — mantle; 14 — posterior gill; 15 — anterior gill; 16 — position of anus in the middle of posterior transverse mantle groove; 17 — visceral ganglion; 18 — heart; 19 — hind intestine; 20 — epithelium of shell; 21 — shell; 22 — apex of shell (embryonic shell); 23 — stomach; 24 — muscle of shell; 25 — esophagus; 26 — pleurovisceral cord; 27 — most anterior point in groove of mantle; 28 — anterior part of mantle cavity; 29 — eye; 30 — tongue; 31 — buccal cavity; 32 — snout; 33 — sac of radula; 34 — section through mantle margin with a weak fold of shell (36); 35 — section through mantle margin with a more strongly developed fold of shell.

marginal growth is known as the ostracum or prismatic layer. Both layers consist of an organic substance (conchin) with deposits of calcium carbonate. The ostracum is naturally weakest at the apex (i. e., at the embryonic shell) and becomes gradually thicker towards the margin. The layers of the hypostracum (nacreous matter), on the other hand, grow in number and thickness from the margin to the apex. In many Eumollusca these two typical layers are covered by a third, the periostracum, which is formed by secondary deposits on the outer side of the ostracum (Figure 6, p. 53).

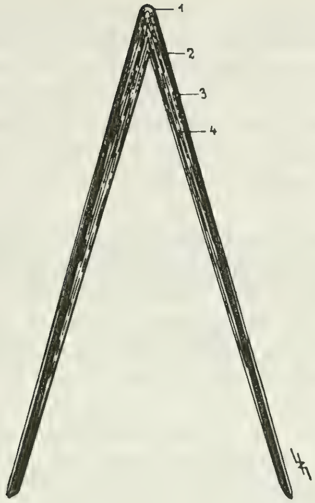

FIGURE 6. Diagrammatic median section through the shell of a typical eumollusc:

1 – embryonic shell; 2 – periostracum; 3 – ostracum; 4 – hypostracum. The hypostracum becomes thicker toward the apex because the first formed nacreous layer does not reach the present margin of the shell. The ostracum, however, becomes thinner in this direction because the young animal built a weaker shell; a secondary thickening of the shell is not possible. The periostracum becomes thicker towards the free margin of the shell if the shell fold (which secretes it) overlaps only slightly (cf. Figure 5).

The entire shell is formed by the epithelium of the shell (20), an epidermal layer adjacent to the shell, but not grown together with it. The ostracum is produced by the outer layer of the epithelium, the hypostracum by its other part, by differentiated glands. The shell fold produces the periostracum.

The marginal areas of the shell epithelium belong to a thin, annular skin fold which hangs free from the visceral mass and adheres to the shell. This is the primary or skin mantle (13). Between the skin mantle and the body lies the mantle cavity (10). The mantle cavity opens outward in the ring-shaped mantle slit. The mantle cavity is narrow anteriorly (28) and laterally and its deepest part is a simple "mantle groove" (27). It widens posteriorly so that the inner boundary of the mantle cavity forms a wide plane known as the roof of the mantle cavity (9–16). The anterior mantle groove (9) divides the roof of the mantle cavity from the body, the posterior groove (16) from the mantle; both grooves meet laterally in the simple mantle groove.

The gills, or ctenidia (14, 15), are situated in the posterior part of the mantle cavity, attached to the roof of the mantle cavity. This "axis" is an apically tapering plate (epithelial fold). The afferent vessel is situated at the median margin of the plate, the efferent vessel at the other margin. Between them there are secondary folds alternating at both sides of the
53 gill axis. These are the "lamellae of the gills." Each basis of the gill is accompanied by the opening of a coelomoduct (renal-genital opening).

The above parts of the body, situated on one side of the line 3–27 in Figure 5, form a natural morphological entity which is connected with the shell and is named shell sac or mantle sac. It contains the main "vegetative" organs. The other part of the body or cephalopodium contains the locomotory organs and the main neural and sensory centers (oesophageal ring (1, 2, 3); statocysts (4) and eyes (29)). This is the "animal" part, which is functionally distinct from the "vegetative" part. The cephalopodium is often divided into head and foot (5), but we shall not attempt to determine whether such a division is typical (cf. Naef, 1911, pp. 85–86). Head and foot are closely associated in typical Eumollusca and indistinguishable in many cases.

The head bears a pair of invaginated (open) or vesicular eyes (29) and continues in a snout (32) in which the mouth opens. The typical structure of the foot part is very problematic. At any rate, I do not assume a simple creeping sole as the basic form for Eumollusca. A fuller development of locomotory-sensory appendages is more probable, but this does not appear in the scheme.

The figure explains the inner structure and shows clearly the major aspects of the typical organization. To be noted is the paired "shell muscle" or cephalopodial retractor (24), its diffuse origin in the cephalopodium (6) and its insertion on the inner side of the shell (7). The insertion is formed by the shell epithelium, the characteristic transversely fibered structure of which at this point provides a firmer connection with the shell than could be achieved by mere adhesion.

54 As regards the change or the "metamorphosis" of the conditions shown in the scheme, we will mention only one point. The formation of the periostracum as defined above (p. 52) presupposes at least a partial folding of the mantle onto the outer side of the shell for some time. This is achieved by a special skin fold which originates at the mantle margin and is called the "shell fold." Such a fold may cover the shell to a varying extent and even enclose it completely, forming secondarily an inner shell. This condition, which is characteristic for all dibranchiate cephalopods, cannot be described simply as growth of the mantle around the shell. The mantle takes part in this process only in providing the shell fold.

e. NORMAL ORIENTATION OF THE BODY

The general orientation of the body as shown in the scheme permits recognition of anterior and posterior, dorsal and ventral parts. This condition is characteristic for other molluscs, but in the normal position of the body of a cephalopod, the shell apex is directed more or less posteriorly and the cephalopodium anteriorly. The posterior side of the schemes thus becomes ventral, and the anterior side dorsal. The posterior gill then becomes the lower, the anterior, the upper gill. Similarly, the posterior mantle groove becomes the lower, etc. This natural ("physiological") position of the body, usually assumed during swimming, is of basic importance for the distinction between upper, lower, anterior and posterior in the following text. Where another morphological orientation takes place, it will be stressed. This orientation should not be applied generally, as was done by Land and Hescheler (1900). This would mean ignoring the natural orientation of the body, and would cause confusion without morphological clarification. The topographic relationships in molluscs are much too complicated (e. g. torsion and detorsion, regulation of the shell position in gastropods; Naef, 1911) and variable for general orientation to be of any morphological help. Distinctions like anteriorly-posteriorly, ventral-dorsal or right left do not provide a significant comparison. A differentiated treatment of the problem of position is necessary, which is easy and natural in our case.

55 5. THE RECENT GENUS NAUTILUS AND THE FOSSIL TETRABRANCHIATA

Contents: a. Nautilus. General form and shell. Suture lines. Form of soft parts. Mantle organs. – b. The fossil Tetrabranchiata. Conclusions.

a. NAUTILUS

Although the genus Nautilus is not represented in the Mediterranean fauna, its prominent position among the manifold forms of the class calls for a brief discussion of its characteristics and relationships to the other forms. The description is based almost entirely on my own data, some new and others confirming existing knowledge, especially the comprehensive description of Griffin (1903) of the soft parts and of Appellöf (1898) of the shell, with whom I generally agree, except in the morphological evaluation of some important points.

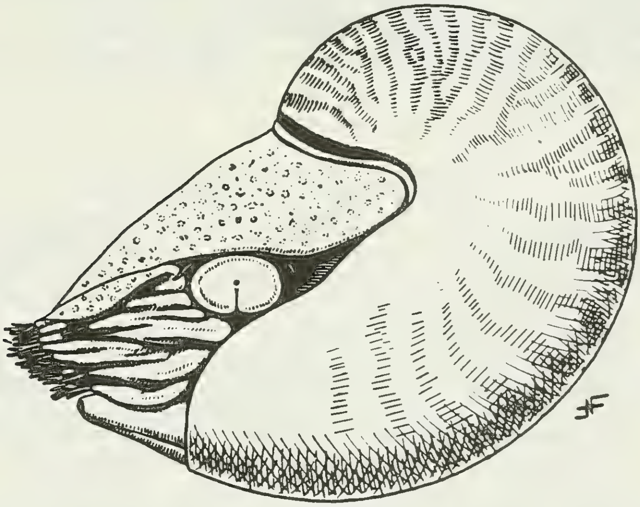

FIGURE 7. Lateral view of Nautilus pompilius in swimming position (half natural size). The shell is without umbilicus, and the free mantle margin is visible dorsally below the "black substance" above the hood. Attention is drawn to the enlargement of the dorsal arm sheaths, toward the hood, the arrangement of the remaining arms, of which 4 are smaller than the others, and the ophthalmic tentacles, the displacement of the eye by the arms and their position with respect to the funnel.

56 Material for the studies on Nautilus was obtained from Pacific islands, including a collection made by Professor Dahl in the 1890s from Ralum (Bismarck Archipelago). Other material, brought by a missionary to Europe and obtained by the station, at Naples, was rather abundant (about 20 specimens) and consisted of immature half-grown specimens which provided some data for embryonic development. The genital organs of the youngest forms, especially the oviduct and nidamental glands, were at a stage passed in Dibranchiata soon after hatching; the gland lamellae, for example, were quite rudimentary and consisted of flat, ridge-shaped elevations (see Chapter 3). The material had been preserved for about 20 years in alcohol, and was not in ideal condition. However, this did not prevent determination of the major relationships, which is the object of this discussion. Jatta had already dissected some of the specimens, all of which were N. pompilius L.

Results of the examination of this material will be published in detail elsewhere; this presentation will be confined to morphological elements, providing data for the determination of the typical cephalopod structure and allowing a comparison with the morphology of the Dibranchiata.

As in all shell-bearing molluscs, the general habitus of the animal is largely determined by the shell which is well known. In recent species of Nautilus the shell may have a wide or narrow umbilicus or be without an umbilicus, and the last whorl of the shell in the mature animal may completely envelop the preceding whorl (N. pompilius), or leave the axis of the coil free on each side (N. macromphalus and N. umbilicatus). The latter condition is undoubtedly the more primitive or typical, since it is also observed in young forms of N. pompilius. In the earliest parts of the shell, the coiling is even looser and the innermost whorl is completely evolute (Figure 9).

The youngest stages of Nautilus have a horn-shaped, curved shell, resembling the shell of fossil forms like Gyroceras, Cyrtoceras and Orthoceras (Figure 8).

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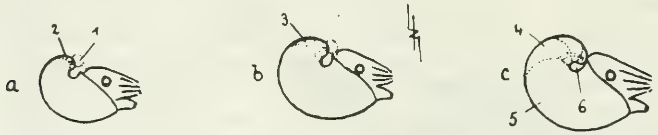

FIGURE 8. Three young stages of Nautilus (hypothetical) (natural size). They are the nucleus of older shells of 3 stages of growth; the soft parts of the young animal or embryo are only indicated. A freshly-hatched Nautilus has 7 chambers, the 8th chamber being much smaller than the preceding ones, as in young Sepia (q.v.). The successive stages have one, two, and three chambers. At the latest after completion of the third chamber, the dorsal margin of the shell must reach the site of the assumed embryonic chamber (indicated by dotted line), which must be removed to permit the second coil to be attached to the first. The first coil is evolute, of Cyrtoceras type, the second coil is attached tangentially to the first, and the next coils show an increasingly involute nature:

1 – hypothetical embryonic chamber; 2 – first air chamber; 3 – second air chamber; 4 – third air chamber; 5 – living chamber; 6 – central hole through Nautilus shell resulting from the initially evolute condition and occupying the axis of the coil.

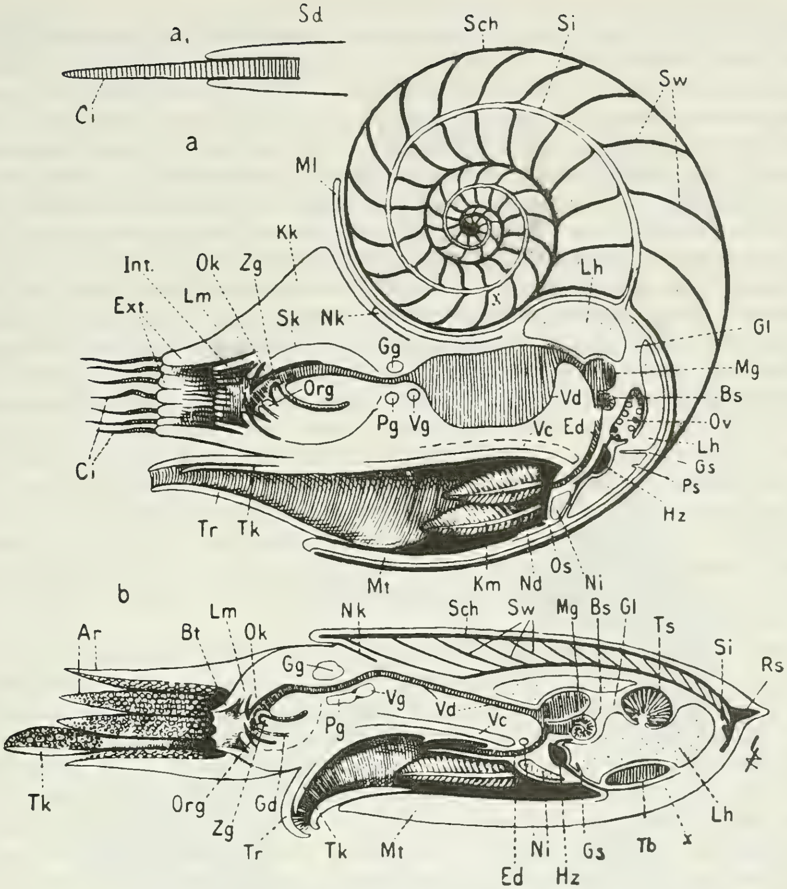
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FIGURE 9. Diagrammatic median section through Nautilus (a) and Sepia (b) for a comparison of the organization of Tetrabranchiata and Dibranchiata:

Lm — lip membranes (outer and inner lip); Ok — upper jaw; Zg — tongue; Kk — hood; Nk — collar; Ml — dorsal lobe of the mantle; Sch — shell; Si — siphuncle; Sw — septa; Gd — poison gland (opening); Gg- cerebral ganglion; Pg — pedal ganglion; Vg — pleurovisceral ganglion; Vd — esophagus; Vc — vena cava; Ed — intestine; Mg — stomach; Bs — caecum; Ov — ovary; Lh — body cavity (coelom); Gs — genital septum; Ps — pericardial septum; Hz — heart; Ni — kidneys; Km — gills; Mt — mantle; Int — sheaths of the inner series of arms; Ext — sheaths of the outer series of arms; Ci — cirri; Ar — arms; Tk — tentacle club; Bt — buccal funnel; Tb — ink sac; Ts — testis; Rs — rostrum; Os — osphradium; Nd — nidamental gland; Org — subradular organ; Gl — gastrogenital ligament.

The coiling of the shell leaves a small empty porus in the axis of the coil between the umbilicus of one side and the other. The central part of this porus persists even when the openings are later closed. The Nautilus shell does not contain a typical central embryonic chamber. Since such a chamber has not been found in larger specimens of the straight-shelled fossil nautilids, its absence has long been regarded as a specific character

of the Nautiloidea in contrast to the Ammonoidea. A typical embryonic
chamber was demonstrated in young Orthoceras by Branco (1879), Clarke
(1893) and Poctà (1902), while it was assumed that in Nautilus this
chamber is later destroyed or lost (Broili-Zittel, p. 495), and this appeared
quite correct to me at first. The shell nucleus is less curved than the
following chambers, in contrast to most ammonites. On completion of the
57 first coil, the shell margin should touch upon the normally developed
embryonic chamber or its hypothetical site. If the animal grows further,
this chamber must be removed. The second coil would then press against
the first septum, which forms the posterior wall of the shell at this stage.
The siphuncle must be retracted from the embryonic chamber (as in
Orthoceras), and close the canal secondarily, probably where it pierces
the first septum. A conspicuous linear depression is in fact always evident
on the outer side of the shell at this point, which according to Hyatt (1893)
is a scar (cicatrix) indicating the position of the embryonic chamber (Broili-Zittel,
Figure 1,075, p. 495). A more recent investigation led me to a different
interpretation: the scar, which is also present in many fossil nautilids,
merely indicates the growth center of the shell, i. e. the site of the primary
"anlage" which grows later concentrically; the first chamber in Nautilus
is actually the slightly modified embryonic chamber which is flat and plate-shaped
rather than vesicular in form. This makes an interpretation of its
secondary removal unnecessary (Figure 8). Other fossil nautilids develop
in a similar manner.*

The formation of the septa of the shell should be interpreted as a modification
of the growth in thickness of other mollusc shells. The septa
develop from the hypostracum (p. 52) and merge directly with the more
distal thickening layers of the shell. The septal necks are derived from
the septa themselves, and the first two septal necks, at least, form septal
58 caeca which envelop the siphuncle completely. In Nautilus, as in many
fossil forms, only the first septal neck is solid; the following necks are
calcified only near the septa ("calcareous"), while the next parts are well
developed but chitinous and enveloped by a weakly calcified, loose sheath. **

59 The sac-shaped body or mantle sac of the animal is situated in the
"living chamber," so occupying it that the ventral and lateral mantle margins
adhere to the inner side of the free shell margin. Above the shell opening
of the living extended animal, the dorsal mantle margin covers an area
covered by the "black substance" which represents morphologically the dorsal
wall of the shell that adheres to the preceding coil. Accordingly, the upper
boundary of the black zone corresponds to the dorsal shell margin which
is covered. (Compare similar relationships in snails, for example, Helix
pomatia.) The animal is attached only to a part of the living chamber.
The concrescence of the epidermis with the innermost layer of the shell is
restricted to the mantle margin and the annulus, a girdle-shaped zone located
behind the origin of the mantle fold which is narrow in its upper and lower

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* After having drawn the above figure, I obtained shells of young fossil nautilids (Cyrtoceras, Gyroceras, Trochoceras, Nautilus, Lituites) which closely resemble recent Nautilus in having no initial vesicular chamber, a siphuncle beginning close to the apex, and a relatively straight initial part of the shell. Other nautiloids differ considerably from this and I intend to use this systematically.

** A detailed description of the structure and development of the Nautilus shell will be found in a synthetic work on fossil cephalopods, which I intend to publish in the near future. In the present book, further details on the subject are only accessory and are outside the scope of this work.

parts and widens considerably anteriorly and posteriorly at the sides. On 60 empty shells this zone can be recognized by the chitinous deposit which makes adhesion possible; if this deposit is removed its position is indicated by a lack of sheen, on contrast to the adjacent areas. In the lateral part of the annulus, especially at its anterior widening, lies the origin of the retractor on each side. Behind the annulus is situated the last septum to which the body is attached except when a new septum is formed. The dividing line corresponds rather exactly to the inner attachment of the septa, called the suture line. It should be borne in mind, however, that there are no muscle attachments on this line, the only one being that of the cephalopodial retractor, which borders on the anterior margin of the annulus and only extends posteriorly to the middle of the zone. The suture lines of the ammonites, whose typical (primitive) forms are closest to Nautilus, are not associated with muscle attachments, although the complex lines would result in a more perfect muscle attachment. The function of the suture lines is different and easy to understand.

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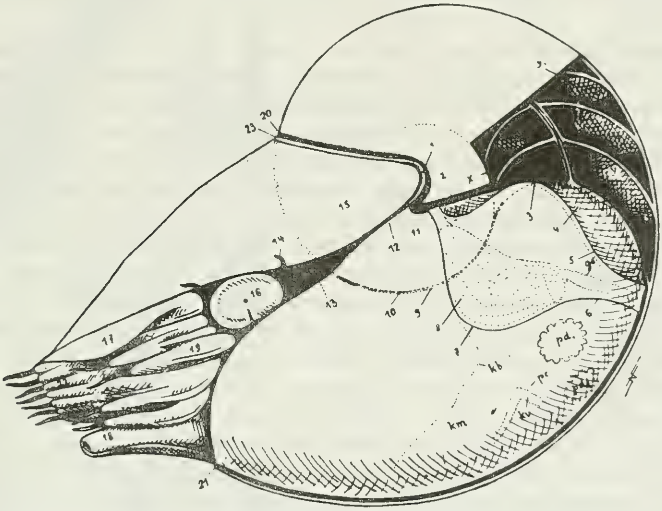

FIGURE 10. Lateral view of Nautilus pompilius. The shell is cut to expose the soft parts, and the last chambers are removed down to the median plane. Fleshy and hard parts of the siphuncle are visible:

y — lower side of penultimate septum; x — upper side of penultimate septum. The last septum is still thin and incomplete. 1 — free dorsal margin of mantle; 2 — posterior boundary of suture line (annulus) which accompanies the attachment of the last septum to the shell wall; 3 — lateral lobe of annulus; 4 — saddle; 5 — posterior wall of the abdominal sac adjacent to the last septum; gs — rudiment of the genital septum; 6 — anterior margin of suture line; 7 — anterior margin of the area of attachment of retractor (8); 9 — dorsomedian border of the mantle sac pressed in by preceding coils of the shell (10); 11 — narrow dorsal part of the annulus; 12 — free margin of shell; 13 — funnel pocket; 14 — ophthalmic tentacles; 15 — hood; 16 — eye; 17 — part of hood produced by the second pair of arms; 18 — funnel; 19 — tactile arms; 20 — border of the black substance (dorsal margin of shell); 21 — ventral margin of shell; 22 — grasping arms; 23 — dorsal margin of shell; pd_1 — upper pericardial gland; pd_2 — lower pericardial gland; pc — anterior boundary of the pericardium and origin of the mantle; kb — branchial attachment; kv — branchial vein; km_1 — upper gill; km_2 — lower gill. The figure shows the relationships between animal and shell.

The strength of the shell depends on the septa, and consequently the safeguarding of the animal against mechanical injury, including high water pressure at greater depths*; the septa also divide the shell in an appropriate manner so that when a chamber is opened by piercing or a break, the animal is not exposed to harmful factors (small organisms and bacteria) nor is the static condition of the shell impaired.

The simple septa strengthen the shell wall effectively but not uniformly, because the areas between the suture lines are left unprotected. A complicated winding, branched suture line would distribute the strengthening effect of the septum over a greater area and uniformly, and also increase the elasticity of the septum. Such a structure improves the resistance of the entire septum to impact and achieves the best possible results with minimal material. Another possible way of strengthening the chamber structure is by increasing the number of septa or thicker walls, which evidently would involve an increase of material and an impaired static condition which would have to be corrected (see the parts on Sepia shells in Chapter 27).

The mantle fold is largely free and can be contracted or expanded while gliding over the shell surface. However, under natural conditions and in healthy animals the mantle fold generally adheres to the shell surface, so that no space is left for small enemies to settle and the outer mantle surface or shell epithelium can function for the thickening of the shell (p. 52).

61 Let us now consider the freely projecting part of the soft body — the cephalopodium. Lateral examination shows a large eye the lateral surface of which represents an oval disk, slightly indented on the lower side and with projecting margin. The contractile "pupil" in the middle is an opening which connects the eye chamber with the water. A groove (ciliated groove) extending from the pupil to the marginal indentation probably serves to remove slime and foreign bodies from the eye. This disk lies on the eyeball which is situated on a thin stalk (Chapter 2) and is inserted in a depression formed by parts of the arms; in this manner, the arm bases and the eye form a more or less uniform surface with the shell margin. Posteriorly and below, the eye depression borders on the funnel pocket, which is almost completely covered by the shell margin in Figures 7 and 10. Below the eye lies the olfactory organ, the rhinophore, projecting externally in a short, tentaclelike process with the openings of two deep pits. The smaller, simpler pit opens dorsally at the base of the process, the other pit is deeper and opens on the process itself, piercing it to the apex and penetrating deep into the head, almost to the statocyst; this pit is lined with sensory epithelium. Only embryological studies can show whether this complex structure is entirely or partly homologous to its simple counterpart in Dibranchiata. There is possibly also a genetic relationship with the statocyst. The arm crown is situated in front of, below and above the eye. All the arms are uniform and consist of a proximal sheath and a distal cirrus (Figure 11). The cirrus is a finely annulated, mobile process, resembling an earthworm with one end inserted deep into the sheath and the other more or less protruding. Morphologically, the sheath is a differentiated arm base which envelops and protects the delicate distal part of the arm.

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* All Nautilus shells show greater or lesser regeneration from injuries of the living chamber. This is a characteristic of a littoral mode of life.

The cirrus can be greatly extended and shortened; it can be retracted almost completely into the sheath or project in its greater part.

This specialization of the arm base into a sheath is specific for Nautilus. The Dibranchiata show no trace of it, which suggests that sheaths were absent in the common ancestors of these groups (Chapter 1). By growing together into complexes of various size, the sheaths make morphological orientation within the arm crown extremely difficult. In these complexes only the distal end with the cirrus opening remains free; the true arm base, including the base of the cirrus, remains concealed. Nevertheless, the following may be recognized (Figure 12, p. 65).

(63)

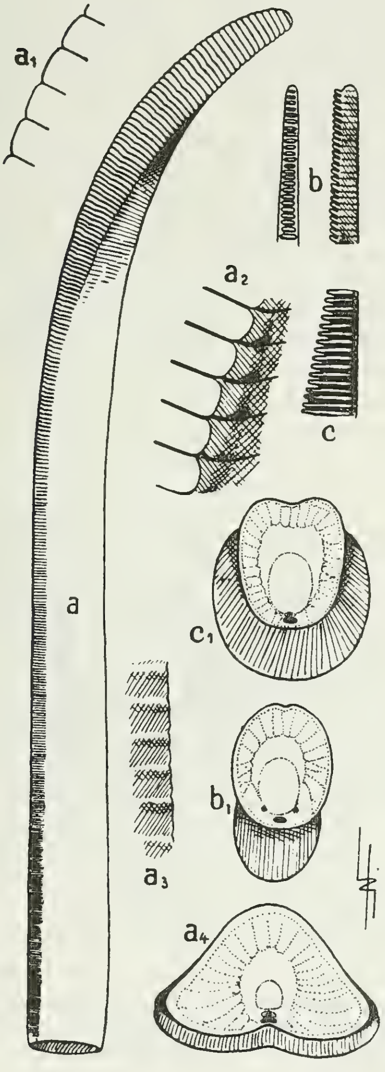

FIGURE 11. Cirri of Nautilus pompilius:

a — cirrus of the outer series of arms (grasping arms) ($^{8}/_{3}$ natural size); a_1 — same, highly magnified in profile; a_2 — transition between the inner and outer surface; a_3 — profile of the proximal part; a_4 — cross section through the distal part; b — sensory cirrus ($^{8}/_{3}$ natural size), inner and lateral aspect, comblike; b_1 — cross section; c — ophthalmic cirrus (apex) ($^{8}/_{3}$ natural size); c_1 — cross section. The cross sections show adhesive pads on the arms within which the oval cross section of the nerve is visible, and the artery and the vein (black) below. Note the variable form of the adhesive pads.

Two very short arms, called ophthalmic tentacles, with short sheaths are situated above each eye, one before it, the other behind it. In front of and below each eye, markedly behind the other arms, are another four arms. These 6 arm pairs differ structurally from the other arms, especially with respect to the cirrus. They are incapable of grasping, and are mainly 62 sensory organs; I have called them "tactile arms." An outer series of strong arms, 15 on each side, surrounds the mouth. The bases of these arms are not arranged in a simple circle, but form a zigzag pattern, so that the outer series can be divided into an inner and an outer row. (In the schematic drawing of Figure 12, this arrangement has been simplified and the number of areas arbitrarily reduced to 6.) There is an inner series of arms which surrounds the mouth. The inner arms, or oral arms, are smaller and more numerous. There are up to 32 on one side in the female and their sheaths are fused into three muscular lobes, two lateral and one ventral. In the male, the ventral lobe is rudimentary or converted into the organ of Van der Hoeven (Figure 12b), and the ventral parts of the lateral lobes (each with 4 cirri) are separated and strongly modified into copulatory organs ("spadix" and "anti-spadix"). The two mediodorsal arm sheaths of the outer series are markedly enlarged, with a tough, warty skin; they extend posteriorly to the dorsal mantle fold to which they adhere over a wide area. Anteriorly they are joined by the second pair of sheaths with a similar surface, contributing to the formation of the hood which can close the entrance of the shell when the animal has retracted inside, like the operculum in snails. (In ammonites the "aptychus" apparently serves to strengthen the hood.) In the quietly swimming animal (Figure 7), the hood protects the animal at least from above. Contraction of the dorsal mantle lobe brings the hood (i.e. the dorsal arms) in direct contact with the shell, particularly with the

(65)

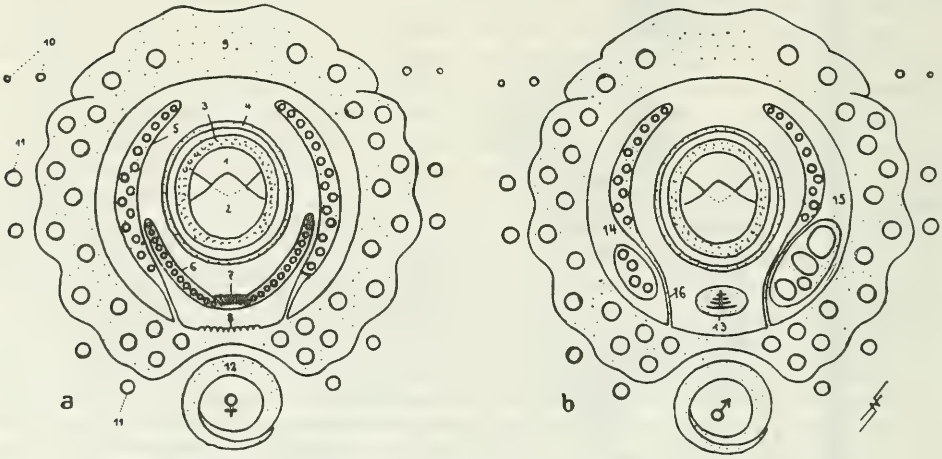

FIGURE 12. Diagram of oral area and arm apparatus of Nautilus pompilius:

a — female; b — male. 1 — upper jaw; 2 — lower jaw; 3 — inner lip; 4 — outer lip; 5 — lateral lobe; 6 — medio-ventral lobe of the inner arm series; 7 — organ of Valenciennes; 8 — receptor for the spermatophore; 9 — cephalic shield passing laterally into the rest of the cephalic sheath, i.e. the product of fusion of the sheaths of all 30 arms; 10 — ophthalmic arms; 11 — tactile arms; 12 — funnel; 13 — organ of Van der Hoeven; 14 — anti-spadix; 15 — spadix.

black substance (see above, p. 59). However, this does not prove that this shell layer is produced by the arms* (cf. Figure 9).

The shell epithelium, i. e. the outer lining of the mantle sac, produces the entire shell. As in all typical molluscs, shell growth is marginal, made possible by the free mantle margin, i. e. the peripheral part of the shell epithelium. The black substance, representing the covered dorsal part of the shell margin, is secreted by the dorsal lobe of the mantle.

All the sheaths of the outer series of arms, including the hood, are fused basally into a head sheath (Figure 12) inside which they show a biserial, zigzag arrangement. The arms of the outer series and sheaths of the adjacent tactile arms (Figure 7), separated by grooves, project above the surface and are curved elbowlike posteriorly, providing protection for the eye. In the female, the inner medioventral part of the head sheath is
63 differentiated to accept the spermatophore during copulation. It has a plicate, glandular surface (Figure 12). Thus, the arm series has important genital functions in both sexes, especially during copulation which proceeds with intertwined arms, mouth against mouth, as in Sepia and many other decapods.

The cirri of the outer series of arms have a typical structure. The base, always contained in the sheath, is almost cylindrical and passes gradually into the extensible part which has a more or less flat, unpigmented inner surface, facing the mouth and a rounded, brown outer side. The cirrus has fine rings, except at the base where the sculpture is indistinct. Proximally the rings are very dense and rather uniform; distally they become in-
64 creasingly wider and on the inner side assume the specific structure necessary for grasping. The incisions become much deeper here and the dense, raised edges form a flattened outer surface. The interior of the prominent parts has a specific musculature which extends from the flat adhesive surface to the rigid, muscular axis of the cirrus, converting each ring into an incomplete sucker or adhesive pad. In view of the large number of rings — about 30 on the projecting part of the cirrus — the combined effect of 30 such cirri in the outer series is considerable. Furthermore, in the largest and best preserved specimens there is always a median groove along the distal part of the prehensile surface of the cirrus. Since the separate pads are closely contiguous and are connected by mucus, the cirrus as a whole can function as a sucker and increase adhesion.

The cirrus musculature is similar to that of the arms of the Dibranchiata, especially in the well defined axial part. The same is true of the nervous and vascular supply of the cirri, as well as their orientation around the head. There is no doubt that each cirrus corresponds to a dibranchiate arm. The adhesive rings are homologous to suckers. This is evident from the embryological development of the suckers (cf. next chapters and Volume II).

The main function of the outer arms, i. e. of the cirri of the outer series, is to capture the prey, which is then transferred to the oral arms. Nautilus feeds mainly on fish; the crops of the specimens I dissected were packed with remains of a sardinelike fish, partly in large pieces. I do not know whether the animal is agile enough to capture such fish or only slow moving species or dead fish. Nautilus was caught with dead fish as bait in weir baskets, so that all specimens had a last meal of this kind, and the stomach contents reveal little about their normal diet. In my view, Nautilus uses its cirri to capture small, benthic animals in their hiding places; such an activity is compatible with the limited grasping power of the arms. However, these arms also serve for creeping. Willey observed that the animal can adhere to smooth surfaces by means of the cirri (Lang-Hescheler, p. 182).

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* G. Steinmann (1890) maintains this without proof. He also states that the shell of Argonauta is produced first by the mantle, and only later by the arms. By such irresponsible statements formulated as actual observations, Steinmann attempts to prove his abstruse view on the origin of Argonauta from the Tetrabranchiata (ammonites) (cf. Chapter 52).

The oral arms are similar in structure to the outer arms, provided they are not secondarily modified into genital or other organs (organ of Van der Hoeven, Figure 12), and they are therefore also adhesive organs. The tactile arms, especially their cirri, are markedly different in structure. The ophthalmic cirri are ciliated in contrast to the other arms (?). Their adhesive pads, however, are highly modified; they surround the cirrus in the form of sickle-shaped lamellae, leaving only the outer side free (Figure 11c, c_1) and their widest part projects markedly from the cirrus, creating a comblike profile (c). The ophthalmic cirri are very short and taper
65 apically more sharply than the other cirri. In addition to their function as sensory organs, the ophthalmic cirri clean the eye socket. The four tactile arms (p. 62) are also unsuitable for grasping. Their adhesive pads do not occupy the entire width of the cirrus, although they project enough to give a comb effect (Figure 11b). The lamellae of the organ of Valenciennes (Figure 12a, N: 7) represent modified cirri and often show transitional forms to the adjacent cirri of the inner series.

The oral arms surround the mouth, which is surrounded by a wide circular fold or outer lip with rather thin edges, like in the Dibranchiata. There usually projects from the outer lip also a second circular fold, the "inner lip" with a thick margin covered with papillae. The outer lip corresponds to the boundary of the primary, embryonic mouth,* whereas the inner lip originates at the interior of the stomodeum and belongs to the anterior part of the
66 buccal cavity. The inner lip usually covers only partly the biting edges of the jaws, and the tongue with the radula, is usually situated on the base of the buccal cavity and can project through the open mouth, so that these parts can be considered as external, although they are described here for practical systematic reasons.

All these relationships are summarized in Figure 12.

The jaws (Figure 13) are large cuticular structures developing from two muscular processes at the entrance of the oral cavity behind the inner lip. The lower jaw projects anteriorly and laterally beyond the upper jaw, so that they act like scissors in biting. Each jaw consists of an outer plate (A) and an inner plate (J), which meet in the angular, protruding biting edge (B). When partly open, the whole structure resembles an inverted parrot beak. Both jaws of Nautilus are covered apically and at the biting edge with a calcareous white substance which is denticulate on the lower jaw. The rest of the jaws consist of chitinous material. The inner plate of the upper jaw is much stronger developed than the outer plate and projects far beyond this; in the lower jaw the proportions are reversed, particularly in Nautilus where the inner plate is completely covered in side view.

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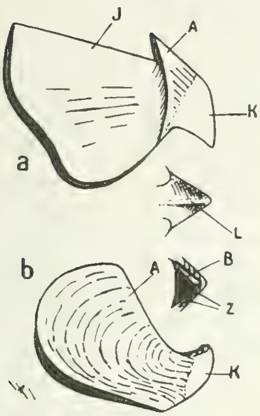
* Easily observed in the development of Dibranchiata.



67 FIGURE 13. Jaws of Nautilus pompilius (natural size):

a — upper jaw with inner plate J, outer plate A, biting edge B, palatine margin L, calcareous coat K; b — lower jaw (same). Note the dentition (Z) along the biting edge (B). Main figures, lateral; small figures, inner view.

As in other molluscs, the radula consists of a bandlike, curved "main plate" covered with dense transverse rows of chitinous denticles. Its posterior end is situated in the radular sac (Figure 9, Zg) where denticles are continually developed as the radula moves forward. The anterior end extends above the tongue where the retrorse teeth widen into a compact brush. This part is strengthened by the "lateral plates" which are connected with the main plate and cover the tongue on both sides. As the animal grows, the radular elements increase in size successively and the radula extends backward at a rate proportional to general growth and inversely proportional to the wear at the anterior part.

The arrangement of the dental rows closely resembles that of typical Dibranchiata. On each side there is a marginal row of flat, transverse, marginal platelets without distinct cusps. Next is a row of long, subulate, curved, outer brush teeth which cover an intercalated row of flat, transverse teeth (intercalary platelets) serving as support, but otherwise without function (this row is invariably absent in the Dibranchiata). Toward the center of the radula there is a row of "inner brush teeth" and further rows of small, short rasping teeth, one paramedian and one submedian. Finally, there is a median row of rasping teeth which project slightly above the preceding rows. (The paramedian row of rasping teeth is absent in Dibranchiata.) Thus Nautilus has 13 rows of teeth compared with 9 rows in typical Dibranchiata. Except for the flat teeth, a radular consists of a basal plate inserted in the main plate of the radula and of a dental process with cusps which extend into the biting edges (cf. Tables 14—16).

The funnel apparatus is strongly developed in Nautilus and some pelagic nektonic dibranchiates in connection with its function. The funnel consists of a muscular lobe which originates behind the bases of the ventral
68 arm sheaths and forms a large tapering sac with the apex pointing outward. When water is expelled from the mantle cavity, the resulting pressure presses the ventral posterior margin of the funnel to the mantle and shell margin (Figure 9, p. 58), closing it completely. A valve on each side of the mantle slit prevents water escaping into the funnel, closing the opening. This is the funnel pocket. The mantle slit (Figure 7) is closed by the collar (Nk) — a membranous lobe which is directed forward and is situated between the cephalic shield and the dorsal lobe of the mantle, adhering to both by its smooth surfaces. (This is homologous to the neck cartilage of the Decapoda.)

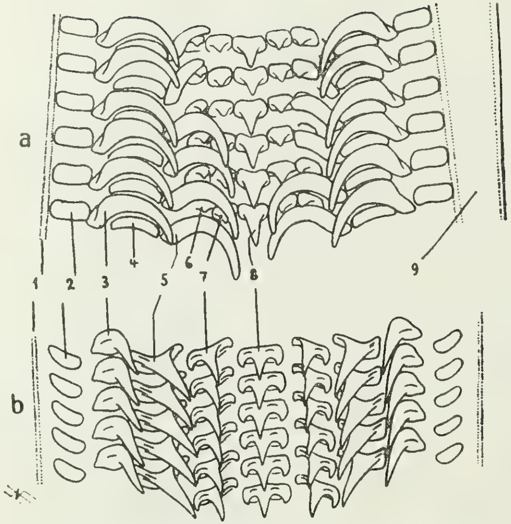


FIGURE 14. Parts of radula of Nautilus pompilius (a) (magnified 6.5×) and Loligo forbesi (b) (magnified 9×). The radulae are flattened:

1 – margin of the main plate; 2 – marginal platelets; 3 – outer brush tooth; 4 – intercalary platelets; 5 – inner brush teeth; 6 – paramedian rasping teeth; 7 – submedian rasping teeth; 8 – median rasping teeth; 9 – lateral plate. The drawings permit a general comparison between Tetrabranchiata and Dibranchiata. The part shown of Nautilus is worn, while that of Loligo is unused. Only the second lower transverse row in Nautilus is intact. The radula of Nautilus widens markedly (as in many dibranchiates), that of Loligo widens slowly and the contrast between brush and rasping teeth is less distinct in Loligo. Otherwise, Loligo shows all the typical characteristics of Dibranchiata.

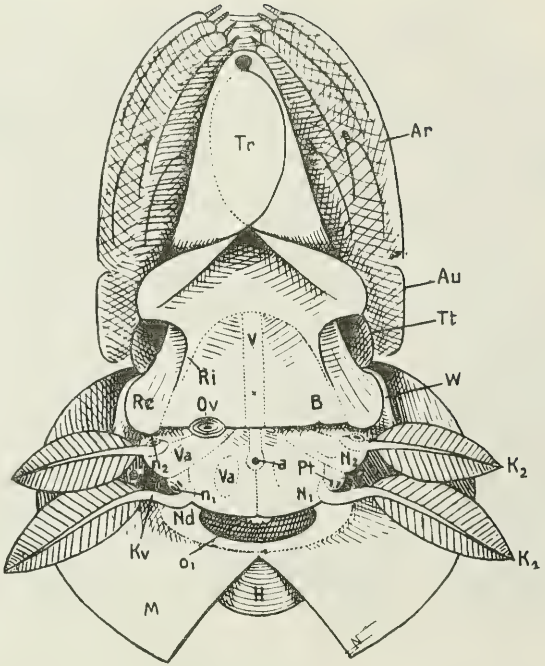


FIGURE 15. Soft body of Nautilus pompilius without the shell, including the anal (abdominal) complex folded back ($^2/_3$ natural size):

M – mantle; K_1 and K_2 – lower and upper gills; Nd – nidamental gland; O_1 – lower osphradium; O_2 – upper osphradium (not marked in figure); Kv – branchial vein; n_1 – lower renal pore; n_2 – upper renal pore; N_1 – lower kidney; N_2 – upper kidney; Va – vein appendages visible through the kidney wall; a – anus; Ov – female (right) genital opening; B – male (left) genital opening of pyriform vesicle; W – swelling bearing gill attachments; Rc – cephalopodial retractor; Ri – funnel retractor; V – vena cava; Tr – funnel; Tt – funnel pocket; Au – eye; Ar – arm sheaths.

In the umbilical region of the shell, the collar passes into the funnel sac where the mantle cavity is very narrow and shallow. The funnel pocket and funnel form together a large, saclike organ. We assume that this organ can actively expand and receive a large volume of water through the aper-
69 ture between the mantle margin and its own free edges. As the whole sac contracts from the front, the free edges are pressed against the mantle and the water is ejected out of the funnel. The resultant repulsion provides energy for movement in a direction opposite to the opening (see Chapter 1).

Another factor comes into play for more powerful propulsion. By the contraction of the cephalopodial retractors the whole anterior part of the body is retracted to some extent into the living chamber and this reduces the volume of the mantle cavity behind the inner opening of the funnel (and that of the funnel itself).

A third possibility of obtaining locomotory energy appears first in the Dibranchiata and consists of contraction of the mantle, which in Nautilus is thin and membranous and adheres to the inner side of the shell (cf. Chapter 2). The intake of water into the funnel and mantle cavity activates another valve situated in the distal part of the funnel. This funnel valve (Figure 9, Tk) closes the funnel opening during inhalation and regulates the intake of water through the mantle slit.

The base of the mantle cavity is of particular morphological interest. While it is very narrow dorsally and closed by the collar and still quite shallow laterally in the umbilical area, the cavity becomes much wider and deeper ventrally (Figures 9 and 10). A posterior lower plane bordering on the mantle cavity corresponds to the roof of the mantle cavity in the molluscan scheme (p. 52). Attached to this is typically a complex of organs folding upon the body just like the mantle, so that its parts become situated ventrally and behind the deepest part of the mantle cavity (Naef, 1913, p. 387, etc.). I called this area at first the anal complex, but later changed this to abdominal complex, which is more suitable and can be better applied to homologous parts of the Dibranchiata. The abdominal complex can be folded back together with the mantle (Figure 15) or separated from the deepest mantle slit as shown in Figure 16. Naturally, what appears here to be transversely extended is, in fact, curved together into a horseshoe.

The abdominal complex is curved back like the mantle, but this condition which I have named "retroflexion" (Naef, 1913, p. 86) should not mislead us into thinking (as Griffin did) that the abdominal complex belongs directly to the mantle and that its organs lie within the mantle. The mantle is actually a clearly defined morphological entity, while the abdominal complex contains numerous organs and its connection with the mantle is only topographical. The same is true of the position of the kidneys, gill bases and other organs in snails, mussels and Chiton with respect to the mantle.

The upper mantle groove (Figures 15 and 16) is not straight but curved in a wide arc on each side before the large points of attachment of the cephalopodial retractors. The part of the groove situated between these points is
70 almost straight; anteriorly and upward it delimits the overhanging complex. Interrupted by the gill bases, the lower mantle groove runs downward and separates the abdominal complex from the mantle. The gills originate in this groove, each receiving its afferent branchial vessel from the abdominal complex (Ka) and returning an efferent branchial vessel to it (Kv). There is a close relationship between the gills and the abdominal complex.

A fleshy fold passes laterally and upward along the mantle groove, from the base of the outer side of each gill (Figure 16). On each side, both folds are fused into a flat ridge on the mantle (Figures 15 and 16W). These branchial attachments displace the gill bases mechanically to the side below the attachment of the cephalopodial retractors. Embryological studies of Dibranchiata and comparison with other molluscs show that the branchial attachments are not primary parts of the gills. In some young stages of Dibranchiata the branchial attachments resemble those of Nautilus and only attach the gill base to the mantle; this leaves the whole distal part free, although later the attachments grow along almost the whole organ. In still earlier embryonic stages, the branchial attachments are absent and the gill is directly based in the embryonic part corresponding to the abdominal complex without connection with the mantle (cf. Plate XVII and Vol. II).

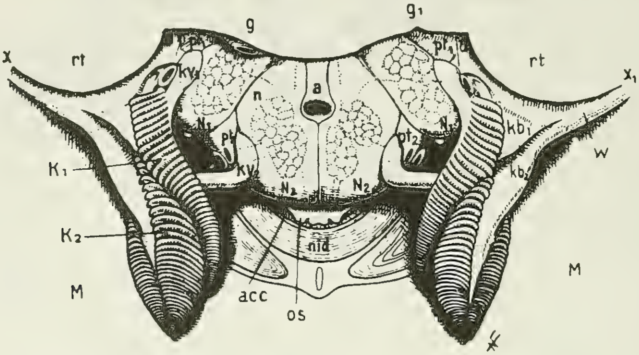


FIGURE 16. Separated abdominal complex of a young female of Nautilus pompilius, flattened ($^1/_2$ natural size). The upper margin (cut) coincides exactly with the oral mantle groove x, x_1. The lower mantle groove follows the designations kb_1, N_1, pt_2, kb_2, N_2.

rt — attachment of the cephalopodial rectractors; g — genital opening; g_1 — opening of pyriform vesicle; n — branchial nerve; a — anus; N_1, N_2 — upper and lower renal sacs; pt_1 — area with opening of gonoduct; pt_2 — area with opening of pericardial funnel; kb_1 — root of the upper branchial vein, near the upper renal pore; kb_2 — root of the lower branchial vein, near the lower renal pore; acc — opening of the accessory glands; nid — nidamental gland area; os — lower osphradium; M — mantle; K_1 — upper gill; K_2 — lower gill; $x - x_1$ — upper mantle groove.

The anus, surrounded by characteristic wrinkles and papillae, is situated in the middle of the abdominal complex. I assume that this is not its primary position which it occupies in many other molluscs (Chiton, Gastropoda, Lamellibranchiata), at least at first. in these forms (16 in Figure 5, p. 51), the anus is situated close to the origin of the mantle or the intestine passes secondarily for some distance along it. In predecessors of cephalopods
71 and embryos of Nautilus, the anus probably lies in the middle between $N_2 - N_2$ in Figure 16 and was then displaced toward the upper mantle groove. Beginning in Nautilus, this topographical displacement is further continued in the Dibranchiata. This may be assumed to be an important step toward

an orientation in the complex of organs since it distinguishes morphologically between anterior and posterior parts in comparison with the typical Bilateria. The intestine passes close to the surface on a stripe (Figure 16a) extending from the anus to the upper mantle groove. This stripe should actually extend to the lower mantle groove, and would mark the morphological longitudinal axis of the complex, as it is only the retroflexed posterior end of the animal (cf. Naef, 1911, p. 85, Figure 3; 1913, p. 282, Figure 6). For the following discussion we shall orientate the complex morphologically, to facilitate comparison with other molluscs (Figure 5). "Anterior" is then what was usually "upper," while "posterior" is "lower" in the sense of physiological orientation (p. 54).

The surface of the abdominal complex or roof of the mantle cavity (p. 52), visible in Figures 15 and 16, is of particular morphological interest not only in Cephalopoda, but also for comparison with other molluscs (this will be discussed later). This surface is divided into a number of areas determined by the position of the different organs situated below the surface. On each side there is an area marked N_2 corresponding to the larger, posterior renal sac, and an area N_1 occupied by the smaller anterior renal sac; kb_2 corresponds to the basal swelling of the posterior branchial vein, kb_1 to that of the anterior branchial vein. Both areas are joined by a third (marked pt_2 and pt_1) at an angle and bearing an opening, the actual or morphological value* of which is that of a coelomic opening. The posterior pair of these openings is situated close to the renal openings and even united with them on common papillae in certain conditions of contraction. This pair of openings connects the pericardium directly with the mantle cavity, the pericardial funnel (Naef, 1913). The anterior pair differs on each side and is distant from the corresponding renal opening on the left and right. On the left side (right in the figures), a small opening situated in the mantle groove, slightly inward and above the renal porus, leads to the piriform vesicle; it is considered generally as a rudimentary gonoduct. Correspondingly, on the right, lies the female genital opening which in the adult animal forms a wide slit covered with characteristic concentric wrinkles on a large papilla, and continues deep into the opening to form the oviduct gland which produces
72 the egg shell. The wrinkles probably form the inner layers of the oviduct gland, while outer layers develop from the nidamental gland, as in the Dibranchiata.

I showed earlier (Naef, 1913) that both the functional and rudimentary genital openings represent true coelomic ducts and are homonomous with the openings of the pericardial funnel. These openings are not only situated close to the kidneys, ctenidia, branchial vessels and a number of visceral organs, but correspond metamerically (i. e. typically similar) to a number of internal organs; the regularity of this position is impaired only by the longer distance from the renal pores. It was assumed (Lang-Hescheler, pp. 359, 341) and proven (Naef, 1913) that the pericardial funnels became independent by separation from the renal pores and that their primary opening led to the renal sacs near the pores, as in other molluscs. The gonoducts presumably moved some distance further in the same direction, and their openings were displaced away from the renal pores. An apparent objection to this view (cf. Naef, 1913, Figure 12) is the presence of the mantle vein near the surface and between the anterior renal pore and genital openings. Embryological studies show that this vein moved here secondarily, so that there is no valid objection to the assumed displacement of the genital organs as indicated. (It will be shown elsewhere that there is also more significant evidence from other molluscs in favor of the supposition of a primary metamerism or dimerism in the Mollusca.)

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* Morphological value: a structure is homologous to another showing the typical configuration of structures of this category; the second structure then indicates the morphological value of the first.

In the male, there are ducts leading from the points corresponding to the genital openings of the female to a median papilla (position marked with X in Figure 15 on the vena cava v), which was erroneously considered as the penis. The ducts unite here into a single opening. On the right, the duct is directly connected with the gonoduct, forming a complete genital duct. On the left the duct is closed, without connection with the rudimentary genital opening. These distal parts are not comparable with the distal parts of the male genital ducts of Dibranchiata, and are special characters of Nautilus (cf. Naef, 1913, Figure 14, p. 406).

The osphradia of Nautilus are characteristic papillae the function of which is perhaps (?) to check the quality of the inhaled water. There are two pairs of osphradia. One osphradium is situated on each side between the renal pores of the same side, forming a rounded lobule; the others form a group of 4 median elevations on the lower margin of the abdominal complex (Figure 16, os). The lateral elevations of this lobe are probably metameric homonyms of the anterior osphradia. However, the morphological and physiological value of these structures is doubtful.

The gills (Figure 17) resemble in principle those of Dibranchiata, and are symmetrical, at least in the "anlage." They differ from the general form by extending transversely, in lacking a separate branchial gland in the fleshy axis, and in their strictly basal branchial attachments which are fleshy and
73 not membranous as in the Dibranchiata. The afferent vessel (2) is situated very deep, while the efferent vessel (1) crosses the inner side of the gill; basally the vessels cross each other, creating the impression of a torsion (such a relation could be proven by comparison with Chiton and Gastropoda!). Between the afferent and efferent vessels lies the branchial axis, which is a thin plate at which the respiratory part of the branchial lamellae is attached, each lamella being situated between two lateral branches of the main vessels. The branchial lamellae alternate regularly, as in most molluscs, and are connected by skin folds with the fleshy axis. Each primary branchial lamella bears secondary lamellae in the form of ridgelike elevations situated close together and arranged as alternating folds on each side of the lamella. Each of these ridges receives a deep afferent vessel and returns a superficial efferent vein. Alternating incisions divide the secondary lamella into tertiary parts with a similar vascular supply.

A characteristic condition of Nautilus are the nidamental glands of the female, which appear late in life on the mantle area bordering on the abdo-
74 minal complex. At first (Figure 16, nid) they represent a continuous system of low ridges extending from one side to the other. Later (as I observed in immature specimen), the marginal ridges form a fold which envelops the whole complex, forming an open pocket (Figure 15, Nd) which contains the glandular lamellar system of the original ridges. This large gland is unpaired, but the lateral parts of the pocket are much deeper than the median; if the median part becomes rudimentary, 2 sacs with glandular lamellae are formed and these are comparable to the nidamental glands of Dibranchiata. However, there is a marked contrast in position.

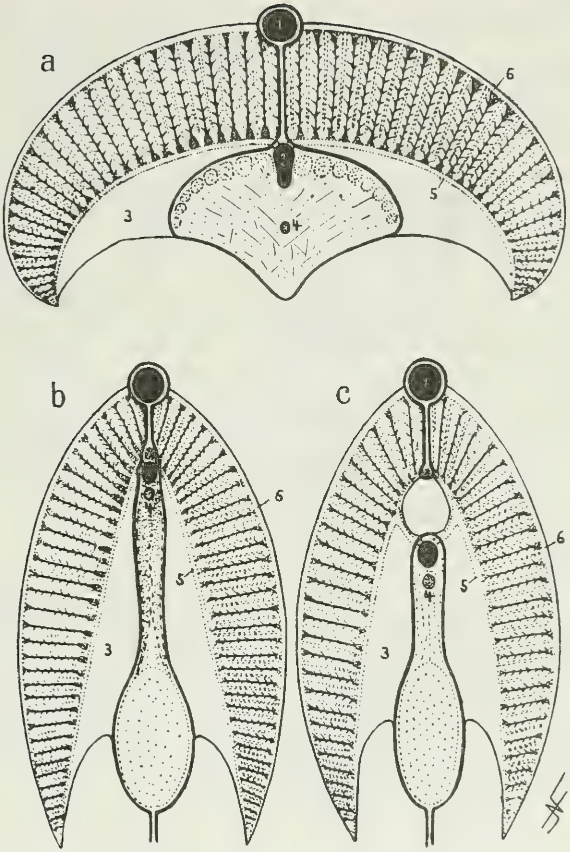

FIGURE 17. Diagrammatic cross section through gills of Cephalopoda:

a — Nautilus; b — Sepia; c — Loligo. 1 — branchial vein; 2 — branchial artery; 3 — ligament (of a single branchial lamella); 4 — nerve; 5 and 6 — artery and vein of a branchial lamella. The dotted area in the lower part of b and c denotes the branchial gland situated in the solid "branchial axis" which passes into the branchial attachment. Characteristic of Nautilus (a) is the absence of a branchial gland in the fleshy axis, in which longitudinal muscles are clearly visible; in c, the perforation of the branchial axis between 1 and 2.

b. THE FOSSIL TETRABRANCHIATA

The organization of the fossil Tetrabranchiata can only be discussed in close connection with Nautilus, but differently for the various groups. The primary organization of the Ammonoidea closely agrees with the above description, at least as regards the shell structure. The earliest ammonites are so similar to Nautilus that they must be considered its closest relatives, if not the ancestors, of the true Nautilidae. The ammonites with modified shells probably had a different soft body, although no specific conclusions can be drawn. At any rate, neither Nautilus nor the related Ammonoidea are directly connected with the origin (type) of the Dibranchiata.

However, Nautilus belongs to the central group of Nautiloidea, although its position there is much less certain than its relationship to the typical ammonites. Genera like Orthoceras, Cyrtoceras and Gyroceras certainly show at least the way in which the coiled Nautilus shell has evolved from the straight Orthoceras-like shell. Unfortunately, there is no direct information about the soft parts of these forms, and only indirectly, by a critical study of the correlation between shell form and soft body in Nautilus can some characters be interpreted as necessary adaptations or mechanical consequences of the shell form, while other characters have to be considered as an ancient inheritance or its metamorphosis. The latter is especially true for characters shared by the Dibranchiata which, in the last analysis, must have developed from the same root. These include peculiarities of organization not present in the Dibranchiata, but which must be assumed for their ancestors on morphological grounds (i.e. typical correlations and embryological data).

Some secondary characters of the Nautilus form can be excluded in this manner, first of all, for the straight Orthoceras-like ancestral forms of the
75 Nautiloidea and also for the common ancestors of Tetrabranchiata and Dibranchiata (which may be identical or even more ancient than the former). This argumentation also eliminates as possible ancestors a number of fossil forms grouped around the genera Piloceras and Endoceras, since the structure of the siphuncle and other shell characters in these forms differ markedly from those of all other cephalopods. These two genera possibly (or probably) represent a more ancient type than the ancestral form of the other groups.

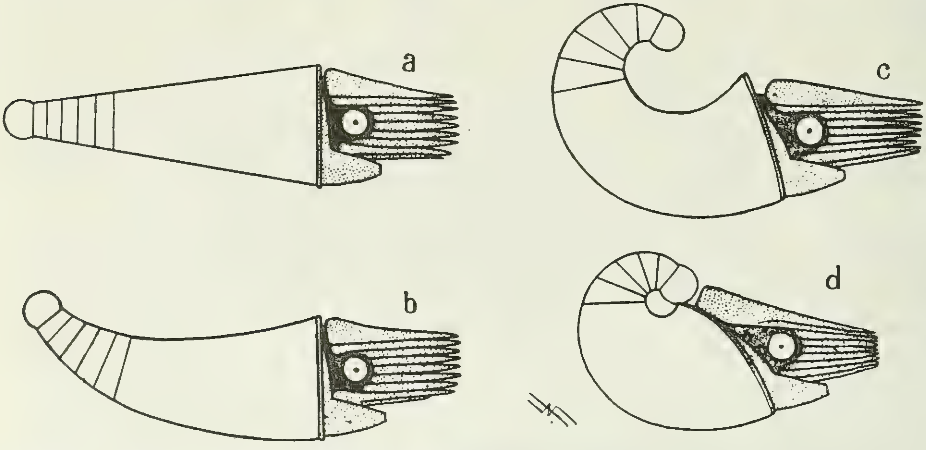

FIGURE 18. Transition of straight Nautiloidea into the typical Nautilus form and reconstruction of the former from relationships in the latter. Four diagrammatic figures of young forms:

a – Orthoceras-stage; b – Cyrtoceras stage; c – Gyroceras stage; d – Nautilus stage. The figure illustrates the modification of the soft body as a result of the coiling; these changes disappear gradually in the early stages. Instead of vesicular initial chambers, those in stages b and c must have been flat and bowl-shaped (pp. 57, 58).

The following characters are apparently secondary consequences of the specific shell structure in Nautilus:

1. the characteristic, dorsally impressed form of the posterior body inside the living chamber (Figure 10);
2. the formation of a special dorsal mantle lobe adjacent to the black substance (Figures 7 and 9);
3. the characteristic form of the collar (Figure 9);
4. the structure of the hood, at least in the final stage. (A certain protective function may be assumed for the upper arms already in a straight shell.) (Figure 7).

These characters are the result of a secondary involution of the early coils into the later coil, the cavity and mouth of which encroach upon each other in the process.

76 On the basis of comparative studies of Dibranchiata, the following characters of Nautilus can be excluded as possible characteristics of the ancestral forms of the group:

1) the differentiation of the basal parts of the arms into tubular sheaths, which are completely absent in the Dibranchiata;

2) the specific complication of the olfactory organ, which in the Dibranchiata consists of a simple pad of sensory epithelium in the young stages or throughout life;

3) the characteristic division and differentiation of the inner series of arms in both sexes and, particularly, the formation of a "spadix" and an "anti-spadix" in the male; it is possible that some arms below the mouth in the female served as recipients for the spermatophores and that they were always transferred by the arms of the male;

4) the separation of the pericardial funnels from the posterior renal pores and the displacement of the genital openings from the anterior renal pores as well as the asymmetrical structure of the gonoducts (p. 71);

5) the formation of an unpaired secondary duct system connected with the primary genital openings and leading to the so-called penis (p. 72).

If these specialized characters of recent Nautilus are ascribed to a common cephalopod type, an unnecessarily complicated path for the evolution of the Dibranchiata would result (see p.10). The phylogenetic approach would lead to a number of unnecessary hypotheses.* Such differentiations would then have to be cancelled and be replaced by others. These difficulties are avoided if the simplest, undifferentiated state is taken as starting point.

By such considerations and assumptions, I obtained an idea of the type of relationships in the Cephalopoda as described in Chapter 1. In the following chapters these relationships will be examined in detail against the available evidence.

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* Influenced by the paleontological nature of the data concerned, I abandoned the terminology of idealistic morphology without applying other methodical principles. Insofar as the systematic connection is concerned, I might as well have stated (p.74): "Neither Nautilus nor the Ammonoidea are direct ancestral stages (p.13) of the Dibranchiata"; or later: ". .... The genera Orthoceras, Cyrtoceras and Gyroceras show at least the way in which the Nautilus shell can be derived from straight shells." This illustrates the difference between an idealistic and phylogenetic approach.

77 *MAIN SECTION*

Chapter 1

CLASS CEPHALOPODA
Cuvier, 1798

Contents: a. Diagnosis. – b. Typical structure of the adult animal. – c. Typical postembryonic development.

a. DIAGNOSIS

Recent and, especially, fossil molluscs, as far as is known, with one or more series of arms around the mouth, a bipartite jaw apparatus resembling an inverted parrot beak, large protruding camera eyes surrounded or enveloped by the basal parts of some arms, and a funnel apparatus which narrows the mantle slit and consists of two large lateral valves (funnel pockets) which open inward, and a ventral funnel composed of two adjacent or fused muscular lobes and serving for the expulsion of water from the mantle cavity. Large, yolk-rich, symmetrically cleaved eggs which develop into young animals without a trochophorelike larval stage. Usually with a calcareous shell, chambered by regular septa, apparently pierced by a siphuncle; shell straight-conical, curved or spiral.

b. TYPICAL STRUCTURE OF THE ADULT ANIMAL
(Including Our Concept of the Structure of the Ancestral Form)

An attempt was made in the introduction to clarify the general principles of systematic morphology and to determine the special application of these principles to our subject. The following discussion will develop this foundation further, although it makes little difference for our purpose if we proceed according to the principles of idealistic morphology or from the standpoint of phylogenetics. At any rate, an attempt will be made to describe the form (ideal, hypothetical or real) from which Nautilus, the fossil Tetrabranchiata and the typical Dibranchiata could be derived in the simplest and most natural way.

78 This has to be done step by step. First, the shell, the most characteristic element of a mollusc, will be studied and its general form characterized. Then an attempt will be made to correlate it with the soft body, i.e. to correct the known structure of Nautilus so that it would fit the typical shell form and to provide the simplest possible connection between the typical structure of Dibranchiata and the general type of molluscs. With

its specific (involute) shell form, Nautilus appears as a much more modified and specialized cephalopod than the type of Dibranchiata established by comparative embryology. However, a number of atypical characters of Nautilus have to be eliminated to obtain the basic form. It should be remembered that the genus Nautilus can be regarded as morphologically primary in view of its great geological age (Lower Silurian), systematic position (Nautiloidea) and great resemblance to embryonic characters of Dibranchiata. This justifies special emphasis on the characteristics of Nautilus, although there are no convincing reasons for it on the principle of typical correlation (see p. 23). Moreover, Nautilus is the only surviving cephalopod with a well developed, completely divided external shell, and the only tetrabranchiate of which the soft parts are known. It therefore provides the basis for the construction of the general type of Cephalopoda.

To save space, not every detail leading to the determination of the type will be discussed. This would involve endless repetition and a complicated network of factual and logical considerations. Such proofs will therefore be given only in the most important parts; in the remaining cases, the explanation, if not self-evident, will be merely suggested. The same deductive method of presentation will be followed in the next general chapters (see p. 41). Thus, the proof of the type valid for a higher taxonomic group will be largely based on what is assumed for the lower groups down to species level. Because of the concise nature of the material, the reader should be able to arrive at pertinent conclusions on the basis of the general considerations if he follows the general train of thought. A part of the following discussion will have to include a repetition of the description of Nautilus.

In many cases the concepts are based on embryological data, and there are therefore frequent references to Volume II where some data on the external development of Dibranchiata are described in comparison with Nautilus as indications of the primary structure of cephalopods.

On the basis of paleontology, comparative anatomy and embryology, the ancestral form of Cephalopoda can only be conceived as a reconstruction of the little known genus Orthoceras, and it is therefore named Protor-
79 thoceras. This excludes temporarily the extinct Endoceratidae, such as Endoceras, Piloceras and related forms with their wide marginal siphuncle which occupies the whole embryonic shell. There is not only the possibility but even the probability that these genera showed still earlier a morphologically primary condition from which the genus Orthoceras may have devolved. Their position is still uncertain (see p. 75).

At any rate, all other recent and fossil cephalopods, especially Nautilus, on the one hand, and the Dibranchiata on the other, have to be traced back to a form close to Orthoceras; the so-called "outsiders" cannot be considered here.

80 After this qualification, it can easily be shown (p. 74) that the typical cephalopod shell is Orthoceras-like. Such shells are known from the Lower Cambrian (Volborthella), while curved and then Nautilus-like shells appear only in the Silurian. It is now established, with respect to the recent Nautilus, that, in contrast to the true ammonites or typical Gastropoda with similar shells (cf. Naef, 1911, p. 94), the juvenile or embryonic shells are at first not tightly coiled but merely horn-shaped like Cyrtoceras. Indirect evidence for this is found in the nucleus of the adult shell

(Figure 8) since very young Nautilus specimens have not yet been obtained. Thus, a less marked curvature has to be regarded as typical for nautiloid shells. Also the earliest Dibranchiata (Belemnoidea) always have straight phragmocones which may be curved in the young, but only in the ventral direction, i. e. in the opposite direction to the curvature of the Nautiloidea. The ancestral form can therefore only be conceived as straight.

A quite clear picture of the soft parts of the ancestral form can also be obtained (Figure 19).

(79)

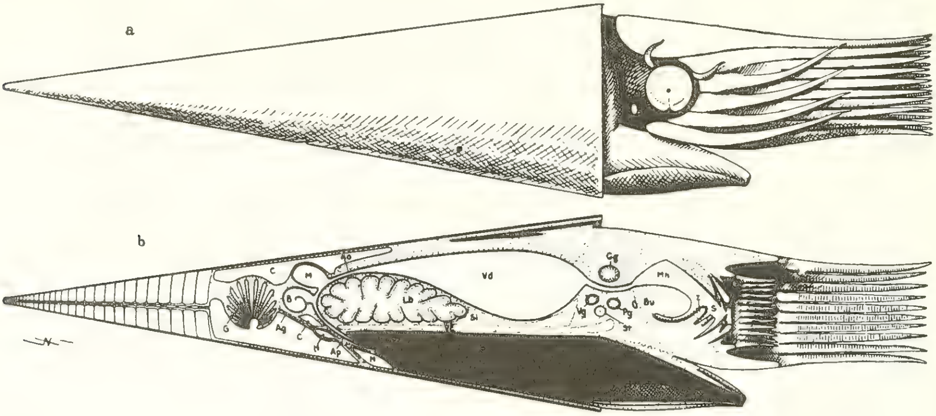

FIGURE 19. Protorthoceras, the ideal or hypothetical ancestral form of Cephalopoda:

a) Lateral view. A Nautilus specimen is inserted and modified to the Orthoceras shell to show in the simplest and most natural manner that it can also be used for the derivation of the Dibranchiata. The number of arms is reduced and their arrangement simplified. Otherwise, the figure shows methodically determined details connected to a naturally possible whole. Note such essential aspects as the conical shell with straight anterior margin, the conical funnel with funnel pockets which occupy the mantle slit, the eye depression surrounded by the arm bases bearing the large camera eye, and behind it the olfactory papilla; the arrangement of the arms is as in Nautilus, but sheaths and cirri are not shown; b) median sagittal section showing the mantle cavity with upper and lower gills and the anteriorly projecting abdominal complex with anus and kidney (N); the collar is attached to the dorsal part of the mantle and the funnel pocket with a valve before the exit. On the head are shown the series of oral arms inside the series of outer arms, as well as the transverse adhesive organs on the arms, the narrow outer lip and wide inner lip, the jaw parts and the subradular organ (S). The shell consists of the embryonic chamber, the air and occupied chambers, septal necks, primary caecum and prosiphuncle. G – gonad (testis), attached by the genital ligament to the last septum of the shell; C – coelom; H – heart; Ag – genital artery; Ap – posterior aorta; N – kidney, with the anus above it; B – spiral caecum; M – stomach; Oa – anterior aorta; Lb – liver; Vd – esophagus (ingluvium); Si – blood sinus; Vc – vena cava; Vg – pleurovisceral ganglion; Pg – pedal ganglion; Cg – cerebral ganglion; Bu – buccal ganglion; St – statocyst; Mh – buccal cavity; Z – tongue with radular teeth; S – subradular organ with sac – homologous to the poison (salivary) gland of the Dibranchiata.

This can be done according to the principles established in the introduction (p. 37). This does not involve a reconstruction of Orthoceras by analogies according to the methods of modern paleobiology (in the sense of Abel, 1917), but the typical must be determined for parts of the structure, as was done with the shell form. The picture obtained is not pure fantasy, because many of the characteristics are general, as the diagnosis shows, while others have proved to be typical according to the principles of morphological primacy.

The general form of the body is determined by the shell, which is a more or less slender cone of varying form in profile,* circular in cross section and with a straight anterior margin. At the apex (see Figure 21, p. 88) the young animal bears the embryonic shell in the form of a spherical or ovoid, slightly inflated initial chamber (see p. 57). The following chambers are divided from one another and from the embryonic shell by watchglass-shaped septa, perforated in the middle by the siphuncle. The siphuncle begins already in the embryonic chamber** surrounded by the primary caecum which is an evagination of the first septum. Similarly, all septal necks are differentiated parts of the septa, which first appear as the posteriorly directed caeca enclosing the siphuncle; at least the first septal necks reach to the end of the siphuncle (Figure 22, p. 89). The primary caecum is connected with the outer wall of the embryonic chamber by the prosiphuncle, a thin, not calcified layer of shell substance. The posterior parts of the septal necks are also not calcified, but chitinous. The rest of the shell is strongly calcified and consists of the following parts: 1) the
81 ostracum, and 2) the inner hypostracum or nacreous layer; the septa and necks also show the typical lamellar structure of the nacreous layer. The outer surface of the shell was probably marked or colored according to the particular environment (indications in fossils!).

From the opening of the conical shell projects the cephalopodium which consists of a number of externally distinguishable parts. On each side there is a large, round, mushroomlike, stalked eye, the chamber of which is filled with seawater as it communicates with the exterior by a contractile pupil (as in Nautilus, p. 61). Around and anterior to the eye (Nautilus, embryos of Dibranchiata, Volume II) are situated the arms which are muscular, whiplike processes the structure of which can be assumed to be similar to that in Nautilus except for the specialized modification of the sheaths of the arm bases (p. 61). The arms probably resembled those of Nautilus in their arrangement. Around the mouth there is an outer series of larger grasping arms which surround an inner series of smaller oral arms, as in the Dibranchiata (Figure 23). It is not known whether the ancestors of Nautilus had tactile and ophthalmic arms or arms of uniform structure. However, a specialization similar to that of Nautilus will be assumed for Orthoceras, since Dibranchiata present no criteria for the modification or derivation of this specialization. However, a perhaps earlier ideal form with uniform arms may have to be assumed (see Introduction, p. 23).

The arms should be assumed to be at least as numerous as in Nautilus. Otherwise, it would be necessary to assume an increase in number within the Nautiloidea. This is the more reasonable because there is the tendency for a decrease in this number in Nautilus where some of the typical arms become sensory organs or auxiliary genital organs. This is also true of Dibranchiata, in which the number of arms decreases to 8, compared with 100 or more cirri in Nautilus.

The detailed structure of the arms may be conceived as follows. All arms resemble the cirri of Nautilus (p. 63) and they present, therefore, a possible starting point for the progressive change taking place in the

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* I chose an average type.

** There are no observations on the origin of the siphuncle in Orthoceras. In this respect, the Ammonoidea resemble Spirula (q.v.) and my considerations are based on this form (cf. Nautilus, p.57).

Dibranchiata (Chapter 2), in which the embryogenesis (Volume II) shows similar stages (Plate IX, Figure 5) in which the suckers consist of simple transverse ridges and are uniserial. The arms are annulated on the outside, except in the proximal part which corresponds to the sheath of Nautilus and is smooth (p. 61); as in Nautilus, the proximal parts of the arms of each series are fused and the annulate appearance of the arms appears as a superficial sculpture without any particular significance.* The inner side of the arms (facing the mouth) differs both from the outer surface and from that of the arms. The incisions are here much deeper and 82 between them are laterally delimited pads (p. 64) with a specialized epidermis and a variety of functional characteristics. All arms were probably tactile and chemoreceptor organs, and this is the main function of the "tactile arms" on which they form sensory papillae (Figure 11b, c); on the outer and oral arms, which I call collectively grasping arms, they appear in a primary and less specialized form. They form here usually adhesive pads with a special musculature in form of a network of crossed fibers, as in the juvenile foot of a snail. The fibers extend in different directions from the muscular axis of the arm to the adhesive surface, which is as flat as the arm surface. Each adhesive pad can probably adhere to a smooth surface, like the foot of a snail, and function as a primitive sucker. This is probably enhanced by a sticky secretion. At any rate, the numerous adhesive pads convert the whole arm into an efficient grasping organ which may be suitable also for creeping (Nautilus).

Also in Protorthoceras the bases of the oral arms may be assumed as strengthened and firm. However, a hood (Figures 7 and 19) was probably not present, since this structure seems to be adapted to a Nautilus-like shell. (The threatened animal probably contracted its arms as close together as possible, with the ends curved inward, as is often observed in Dibranchiata and thus protected at least the most vulnerable parts.)

There are close relationships between arms and eyes. Although stalked as in Nautilus and dibranchiate embryos (see Volume II), the eye bulb probably did not project markedly above the other parts of the cephalopodium, as otherwise this vulnerable organ would have been exposed to grave danger. The surrounding parts project to the same extent and form a protective wall. Protection is provided from behind by the shell and funnel valves, and from the front, above and below by thick, muscular arm bases (see "arm pillars" in Volume II) which project elbowlike from the outer, upper and lower side of the head, where they are fused into a tough, firm envelope or head sheath (Figure 12) around the head which leaves no vital part exposed. These parts form an orbit or socket around the eye in which it is protected without losing its motility. Another part situated in the eye pocket is the olfactory organ, a rounded flat papilla with sensory epithelium, which is present in all Dibranchiata, at least in the young stages, and is the starting point for higher differentiations. In Nautilus, however, it undoubtedly shows an atypical, complicated structure (p. 61).

The sagittal section (Figure 19a) shows an outer series of arms which here too is assumed to be multiserial. Inside this series is a similar series of smaller appendages. This inner series surrounds the mouth,

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* However, this may also be the result of a marked shortening of the arms whereby the skin would form predetermined folds.

which is delimited by a wide, circular skin fold or outer lip from which the
83 inner lip projects in the form of a second circular fold. The outer lip is narrow, thin at the margin and more or less smooth. The inner lip is generally covered with regularly arranged papillae which probably serve as taste organs. The inner lip usually covers only incompletely the biting edge of the jaws. Further back, the subradular organ and rasping tongue are situated on two elevations on the floor of the buccal cavity. At rest they are completely covered. Like the jaws and inner lip, however, they can be projected far outside the mouth, delimited by the outer lip, and appear then as external structures.

The jaws and radula were probably of similar form as in Nautilus (p. 66), the radula with 13 longitudinal rows of teeth which are simple and flat on the outside, while the second and fourth rows on each side consisted of brush teeth (Figure 14).

The funnel apparatus consists of four parts: a dorsal and ventral part and two lateral parts connecting them. The dorsal part is not active and is merely an adhesion and sliding device connecting the movable cephalopodium with the shell through the mantle. Invisible from the outside, the dorsal part is visible in sagittal section (Figure 19) where it appears as a slightly projecting, rimmed, hard and very smooth part of the neck, the "collar," which may have a fine longitudinal sculpture of ridges and grooves corresponding exactly to similar structures on the inner side of the mantle. The mantle, however, continues further back, permitting a gliding retraction of the cephalopodium into the shell in continuous adhesion (like a sledge; cf. Chapter 3).

The ventral part is the funnel tube, which consists, as in Nautilus, of a cone composed of the funnel lobes, i. e. the lateral parts of a transverse, muscular plate on the lower side of the head which forms an angle open posteriorly; these lobes overlap ventrally. The funnel tube is wide open posteriorly, while it ends anteriorly in a narrow opening for the ejection of water. The pressure necessary for this ejection is achieved only by the lateral funnel pockets, which can close the lateral parts of the mantle slit hermetically. The funnel pockets are muscular lobes which originate anteriorly on the body (as visible in lateral view); their free posterior margin is inserted below the shell and mantle margin. The funnel pockets are dorsally connected with the collar and ventrally with the posterior part of the funnel into a pocket which opens posteriorly (Figure 16). Between the funnel and pocket lies the muscular funnel septum which continues posteriorly in a muscular ridge to the gills. This is a still imperfect retractor infundibuli* (see Chapter 2) which strengthens the funnel and attaches it to the body. During swimming, the pressure on the water compressed inside the mantle cavity inflates the pockets which adhere to the inside of the mantle and function as valves. The pockets, however, are not strictly passive. During ejection of water, the musculature of each pocket contracts from the anterior to the posterior part without detaching their posterior margin from the mantle. The funnel tube functions similarly, its posterior margin acting as a valve by being pressed against the mantle.
84 A third process, generating the main impetus during rapid swimming, is the partial rhythmic retraction of the entire anterior part of the body into the

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* Usually named depressor infundibuli, for obscure reasons.

shell, creating a sudden and powerful reduction of the contents of the mantle cavity.* The compression of the mantel-funnel cavity forces a jet of water through the funnel, creating power for movement in the opposite direction. In principle, the direction of the opening is not important; the end of the funnel can be curved down or posteriorly, causing the body to move upward or forward. The pressure generated by the contraction acts uniformly in all directions, but the water jet harnesses this pressure into a definite "desired" direction. (This is the physical-ecological sense of the concept of recoil.)

If the cephalopodium projects from the shell, the mantle-funnel cavity expands; the funnel and the funnel pockets are dilated so that their posterior margin becomes detached from the mantle. At this stage, water can flow in through the entire lateroventral mantle slit. These suggestions on the mechanism of locomotion have to be sufficient for an understanding of the funnel and its modifications within the class. The animal swims mainly posteriorly with the arm tips joined into a cone and operating as a rudder.

Dorsally shallow and narrow, the mantle cavity widens considerably on the ventral side where its configuration resembles that of Nautilus; the abdominal complex is folded forward and is consequently not visible even after complete removal of the ventral half of the mantle (Figure 20a), but all four gills are visible. In form and position, they resemble the gills of Dibranchiata; as in Nautilus, however, they are attached at the base and lack a branchial gland, and the upper gills are smaller but otherwise fully developed. Orthoceras may have had more than two pairs of gills although there is no evidence for such an assumption.

To illustrate the connection with the Dibranchiata, the hypothetical transitional form "Metorthoceras" is drawn in Figure 20b (p. 85). In this form the roof of the mantle cavity and the abdominal complex correspond in position to those of the Dibranchiata. Although such a displacement certainly took place in the ancestors of Dibranchiata, we do not know whether it was present among Orthoceras-like animals or appeared later in the Dibranchus-like animals (Chapter 2). The figure is mainly of instructive interest; it shows all the important parts of the mantle, including those of the roof of the mantle cavity (the abdominal complex) and we apply again
85 (p. 71) the morphological orientation (p. 54) which fully corresponds here to the physiological orientation since the lower parts are in fact displaced posteriorly, etc. Both gill roots are visible on each side, particularly the basal swellings of the efferent vessels (Figures 15 and 16) in front of which are situated the renal papillae. The posterior pair of renal sacs (Va_1) receives the pericardial funnels near the anterior pores (N_1), while the anterior pair (Va_2) receives the gonoducts at the corresponding place (N_2).
86 Thus, the contents of the gonoducts reach the renal pore, which also serves as the genital opening.** Figure 20b shows clearly the anterior mantle

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* Compressed water exerts uniform pressure in all directions. In our case, it acts on the walls of the mantle-funnel cavity. In most places, the pressure is neutralized by equal pressure in the opposite direction; an exception are only the funnel opening and the diametrically opposite point. The resting animal breathes by similar but weaker movements.

** The conditions described here are probably ancient with respect to the latest common ancestor of all Cephalopoda, since the special ectodermal, glandular differentiation of the genital openings (oviduct gland, spermatophore gland) which reappears in the Dibranchiata suggests that the anterior renal pores became separated from these openings already in the common ancestor. In Nautilus the anterior renal pores are well preserved and show no glandular differentiations. If the figure is considered as a transition to the Dibranchiata in which the anterior kidneys are lost, N_2 would indicate mainly the genital opening.

groove, which is the deepest (posterior) part of the mantle cavity, as well as the anus which is here situated closer to the anterior mantle groove than in Nautilus, to illustrate the transition to the Dibranchiata.

(85)

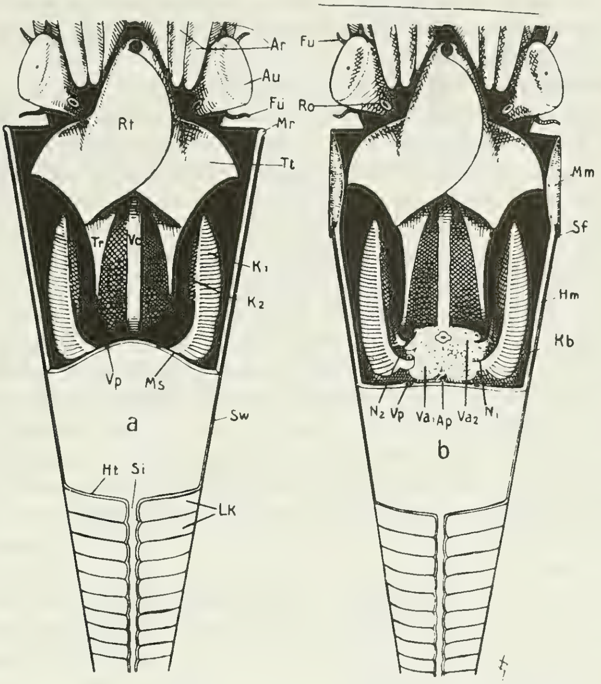

FIGURE 20. Situs of the mantle cavity in Protorthoceras (a) and Metorthoceras (b), a transitional form to the Dibranchiata. The ventral half of the shell and the mantle are removed (the sections are clearly visible). The funnel is formed on the same principle as in Nautilus, and in (b) it is assumed to be stabilized by a postembryonic fusion of the lobes. On each side, the posterior margin of the funnel leads to a "funnel corner" which marks the attachment of the septum on the inside and the origin of the retractor. In (a) the retractor ends in the trunk musculature (shell muscle); in (b) it reaches the shell independently. Two pairs of ctenidia are visible in the mantle cavity. The roof of the mantle cavity (abdominal complex) is not visible in (a) since it is inclined forward against the ventral mantle groove or the ventral attachment of the mantle (section plane) as in Nautilus; in (b) it is displaced as in the Dibranchiata and therefore visible. The ventral mantle groove is situated farther posteriorly than the dorsal groove (Figure 15). (b) shows the development of an imperfect muscular mantle (Chapter 2). Both figures show the position of the prominent eyes with respect to the arm bases, funnel, mantle margin and olfactory organ.

Ar — arms; Au — eye; Fü — ophthalmic arm; Ro — olfactory organ; Mr—mantle margin; Mm — muscular mantle; Sf — shell fold; Hm — skin mantle; Kb—gill ligament; N_2— opening of the anterior kidney, also serving as genital opening; N_1 — opening of the posterior kidney; Va_1 — translucent appendages of the vein of the posterior kidney; Va_2 — same of the anterior kidney; Ap — median pallial artery (cut); Vp — posterior pallial vein; Ms — section through the mantle; K_1 — lower (posterior) gill; K_2 — upper (anterior) gill; Vc — vena cava; Tr — funnel retractor; Rt — funnel; Ht — shell epithelium; Si — siphuncle; Lk — air chambers; Sw — shell wall.

The anus was probably originally situated (see p. 51) close to the attachment of the mantle fold (i. e. where this is cut off in Figure 5). In Protorthoceras, however, we assume that the anus had the same position as in Nautilus (Figure 15), because the Dibranchiata advanced even further in the same direction (Chapter 2). The section shows three vessels entering the mantle: the median posterior pallial artery and the paired posterior pallial veins (Naef, 1913, p. 422).

The idealized Figure 20 shows the funnel retractors in a configuration which would lead to the Dibranchiata. The retractors reach here the shell above the gill roots. Dorsally, toward the interior of the mantle cavity and close to the surface are situated the powerful cephalopodial retractors (shell muscles), which pass laterally above and behind the gill roots (covered by the lower branchial band) and reach the shell (see Figures 20a and 15).

Like Nautilus and the Dibranchiata, Protorthoceras is assumed to show marked sexual dimorphism in addition to the structure of the genital organs, which lie inside the body and the mantle cavity. Thus, the mature female is assumed to have had a larger living chamber than the male. As mentioned above, Protorthoceras probably had the necessary arrangement for receiving the spermatophores on the ventromedian part of the arm series; such an adaptation is also found in Nautilus as well as in the Dibranchiata. In the male some arms were probably adapted for the transfer of the spermatophores and embracing the female. Such modifications are known as hectocotylization,* an extension of the definition by Steenstrup (1856) which applies to the Tetrabranchiata as well. No details can be given for Orthoceras.

The true and accessory (doubtful) nidamental glands were probably similar to those of Nautilus (Figures 15 and 16), although no specific details can be given (p. 74). At any rate, these glands were unpaired or connected in the middle.

87 The mode of life of Protorthoceras was probably similar to that of Nautilus. Protorthoceras was probably a good swimmer, but was benthic and littoral and therefore also a good creeper. It probably fed on dead and living, small sluggish bottom dwellers.** Its shell form facilitated rapid movement in a straight direction, but made turning rather difficult in contrast to the compact shell of Nautilus, which I consider as an ecological reason for the spiral coiling of the shell, which also has the advantage of improved stabilization of the body. The position of the air chambers above the living chambers (Figures 9 and 18) gives the shell of Nautilus a stable equilibrium in contrast to Orthoceras. The transitional sequence Orthoceras — Cyrtoceras — Gyroceras — Nautilus is also a series of adaptation culminating in Nautilus in a highly successful solution of hydrostatic and hydrodynamic problems. This interpretation is confirmed by its long existence and the capacity for infinite variation of the type in the Ammonoidea.

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* This modification is probably even more ancient. As can be demonstrated in the Diotocardia (Fissurella), the penis of snails is a modified appendage of the cephalopodium (an epipodial tentacle). Consequently, these copulatory organs can be regarded as homonomous to the hectocotylus and spadix. This will be discussed further elsewhere.

** Jaekel (1902) has expressed the curious hypothesis that Orthoceras was a sessile form. This view was completely disproved after Pocta (1902) proved the existence of a typical embryonic chamber in them.

c. TYPICAL POSTEMBRYONIC DEVELOPMENT
(My views on the development of the ancestral form)

To describe the development of a hypothetical animal, such as Protorthoceras, may seem presumptuous. As shall be proven later, such an undertaking is quite possible and can be scientifically justified. A hypothetical but naturally possible animal evidently has an ontogenesis (p. 11) which can be visualized by applying the same principles as used for the adult form. In other words, it is necessary to determine the typical early states, just as the typical final state was constructed.

In this particular case, the factual preconditions for the establishment of a typical course of development are very unfavorable. The size of the eggs and the shell of the adult animal are the only source of information on the early stages of Nautilus (Figure 8); as in most molluscs, the shell contains its early stages and none of the latter is known. The structure of the young Orthoceras shell is known only incompletely (Figure 21). On the other hand, there is a wealth of data on the development of Dibranchiata, which should aid us in this respect (see Volume II).

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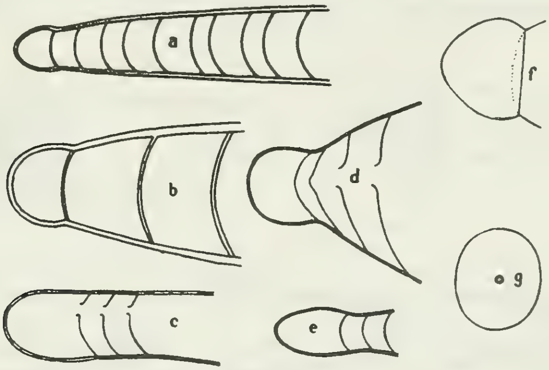

FIGURE 21. Longitudinal sections through young shells of Orthoceras:

a–e – after Poctà, 1902; f, g – after Clarke, 1893. The solidly calcified, embryonic chamber, slightly vesicular in form, is slightly different from the other chambers; the opening angle varies and the septal necks are only partly calcified and incompletely preserved. The septa are not equally spaced. The form represented by (d) probably had a creeping, snail-like mode of life, or swam like a pteropod with the cephalopodium down. Such short conical forms are invariably small. f – lateral view; g – first septum. Compare also Branco, 1885. Bactrites is an orthoceratid!

We assume that Protorthoceras, like all Cephalopoda, hatched in the adult form, not as a larva. Nautilus eggs are even larger than those of
88 most Dibranchiata. The postembryonic development of Dibranchiata suggests, however, that some organs were not fully developed at the time of hatching. (This excludes external characters of sexual dimorphism, which are absent in the young animal.)

The shell of Orthoceras can be reconstructed according to the youngest shells (Poctà, 1902). At any rate, the embryonic chamber and a living chamber formed by the adjacent part of the shell must have been present at the time of hatching.

Nothing is known on the development of the siphuncle and prosiphuncle, which is quite obscure in Nautilus and Spirula and too modified atypically in Sepia to permit any direct conclusions. The prosiphuncle is formed by a part of the shell epithelium which remains fixed long after the rest has become detached from the inner side of the embryonic shell. The siphuncle develops as a process of the posterior part of the body, secreting a hardening but not calcified shell substance even before the formation of the first septum,* while the space created is filled with gas.** These are the preconditions for the formation of the first septum with the primary caecum. Further development involves: 1) a continuous or periodic growth at the free shell margin (ostracum); 2) the deposition of thickening strata (hypostracum) before the annulus; 3) the formation of new
89 septa and septal necks behind the annulus, after the posterior end of the animal had moved some distance forward in the shell tube, leaving behind each time only the beginning of the siphuncle; 4) the formation, by the annulus, of a thin layer which separates the wall from the septa and which belongs to the hypostracum.

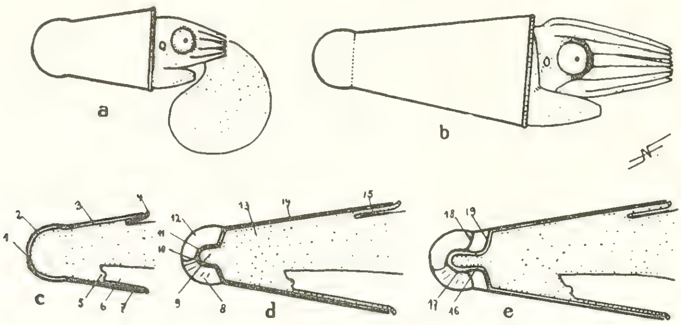

FIGURE 22. Hypothetical development of Orthoceras (about 6 x natural size):

a) – embryo before the formation of the first septum; b) – embryo with one chamber (embryonic chamber); c) – median section through the posterior part of the body of (a); d) – median section through the posterior part of the body of (b); e) – formation of the second septum with the corresponding septal neck. 1 – shell apex (initial vesicle); 2 – shell epithelium; 3 – conical part of the shell; 4 – mantle margin; 5 – anus; 6 – mantle cavity; 7 – mantle; 8 – prosiphuncle, sagittal lamella; 9 – siphuncle; 10 – prosiphuncle, main pillar; 11 – primary caecum of the siphuncle; 12 – embryonic chamber; 13 – soft body; 14 – shell epithelium; 15 – collar; 16 – second septal neck; 17 – first septal neck; 18 – first septum; 19 – second septum.

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* Some young stages of Dibranchiata (Vol. II) suggest that the embryonic chamber (or the posterior part of the soft body) gradually loses its large reserve of yolk, which is replaced with gas.

** This space may be at first filled with a gelatinous substance (as in the embryos of Sepia, Vol. II) which is later replaced with gas. The same may apply to the following air chambers (cf. Appellöf, 1894).

Heterochronisms in the development of the arms may have been evident in such early form as Protorthoceras, as for example in the Oegopsida (q. v.), and this prepared the later progressive reduction in the number of arms; that is, there are reasons to assume that the youngest stages of the ancestral form had only a few arms, and that the other arms developed later. Such a state in the young forms could explain the gradual reduction of the oral and outer arms in the descendants (Dibranchiata), and is very probable in view of the large and varying number of arms in Nautilus (up to 70 oral and tactile arms, 30 outer arms) and their partly rudimentary character.

The arm organs were also probably simpler (p. 81). As in the Dibranchiata (Volume II), the eye pocket was probably formed by the projecting arm pillars, later in development, i. e. in the postembryonic stage. The typical development of the shell shown in Figure 22 is important for the understanding of the shell of the adult and its differences in the Tetrabranchiata and Dibranchiata.

The typical structure of Cephalopoda has changed in different directions, only one of which is represented in the Dibranchiata, the others occurring in the Tetrabranchiata.

90 *Chapter 2*

SUBCLASS DIBRANCHIATA

Owen, 1836

Contents: a. Diagnosis. — b. Typical structure of the adult animal. — c. Typical postembryonic development. — d. Variation of the type of Dibranchiata.

a. DIAGNOSIS

Cephalopoda (p. 77) the shell of which, if present, is situated inside the body covered by a shell fold and enclosed in an epithelial shell sac. The position of the ventral part of the primary mantle and the corresponding shell part of the living wall of the chamber is occupied by a powerful muscular layer — the muscular mantle. Only 8—10 outer arms, with suckers, at least in the young stages. The eye is a closed capsule with an iris fold and a lens, and situated in an orbital chamber which may be open or closed by a transparent skin fold (cornea). There is only one pair of gills with a dorsal branchial gland in its axis attached to the muscular mantle by a branchial band along most of its length. The funnel tube is firmly closed in the ventral median line by fusion of the two halves, its interior partly covered with glandular epithelium (funnel glands). The skin bears typical chromatophores (light and dark) which may produce a rapid change of coloration.

b. TYPICAL STRUCTURE OF THE ADULT ANIMAL

I assumed an ancestral form of all Dibranchiata, a form which I named Protodibranchus, of which a more or less complete picture can be given (Figure 23). This form is not realized in any known fossil or recent form, but its scientific justification lies in the fact that it combines the typical traits of individual parts of the organization of recent and extinct Dibranchiata, obtained by methodical abstraction.

Figure 23 shows the general habitus of the animal. The body is slender, about the size of the drawing, it is swimming and more mobile than the Tetrabranchiata. The skin pigments are situated in typical chromatophores,
91 and not in ordinary subcutaneous connective tissue cells as in Nautilus. The chromatophores are large vesicular cells expanding with the aid of contractile radiating fibers and contracting by their own elasticity, changing the coloration. There are two types of chromatophores: i. e. yellow and light, and others dark with varying proportions of red and dark brown pigment. The combined function of both types creates different

tones and patterns, which are more or less stereotypic and depend on the innervation. The chromatophores are not merely agents of protective coloration, but also a means of communication necessary for gregarious animals. When completely contracted, they appear as small dark dots, not visible from a distance and not appreciably affecting the coloration of the animal, so that the milky, translucent texture of the flesh becomes evident.

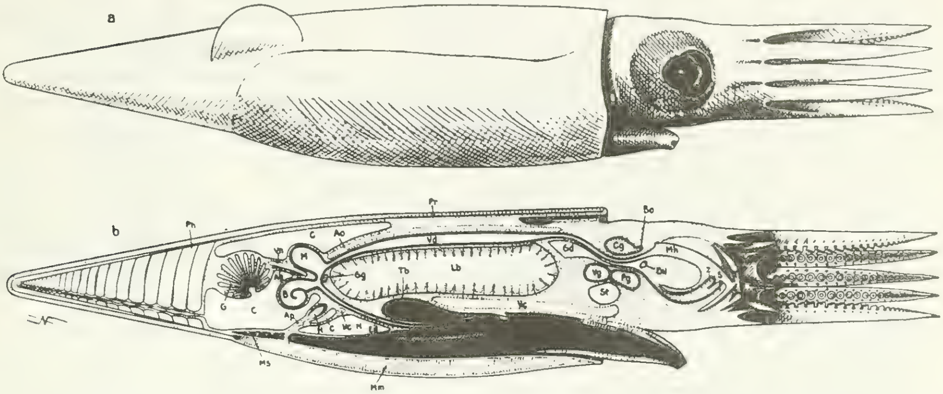

FIGURE 23. Construction of Protodibranchus, the hypothetical ancestral form of all Dibranchiata. Above — lateral view; below — sagittal section. Noteworthy are mainly the relationship between the muscular mantle (Mm) and the shell which is covered only by a skin fold, the position of the fins, the form of the mantle margin; the primary eyelid, the iris; the arrangement and mutual position of the arms, the grouping of suckers on the outer and oral arms, the condition of the outer and inner lip, jaws and radula. Note further the median section through the shell, the dorsal and ventral parts of the mantle cavity and the funnel tube:

Ph — phragmocone; Pr — proostracum; G — testis; C — coelom; Ms — mantle septum; Ap — posterior aorta; H — heart; Vc — vena cava; N — kidney; Ed — intestine; B — caecum; Ag — genital artery; Vn — genital vein; M — stomach; Ao — anterior aorta; Gg — parietal ganglion; Tb — ink sac; Lb — liver; Vd — esophagus; Gd — poison gland; Vg — visceral (parietal) ganglion. St — statocyst; Cg — cerebral ganglion; Pg — pedal ganglion; Bo — upper buccal ganglion; Bu — lower buccal ganglion; Mh — oral cavity; Z — tongue; S — subradular ganglion.

Another element of the coloration is the argentea — an iridescent sheet situated mainly beneach the chromatophores and reflecting yellow-green, reddish, violet and blue-green light caused by the vertical, iridescent guanin platelets in the iridocytes.

92 As in all Dibranchiata, the shell is completely internal; it is enclosed not by the mantle, as usually stated, but by the shell fold which develops from the mantle margin (p. 54). The shell is tightly enveloped by the completely closed shell sac, which is formed by the primary shell epithelium (p. 52) and the also ectodermal shell-fold epithelium, which is secondary, i. e. directed toward the shell. The structures produced by the primary epithelium are homologous to the tetrabranchiate shell and resemble it closely. Secondary shell parts are deposited by the secondary epithelium on the outside of the "primary shell."

In Protodibranchus the secondary components probably consist only of a stratified, crustlike coat named sheath or periostracum (p. 52).

The main character which determines the habitus of the animal and distinguishes it physiologically and ecologically from the Tetrabranchiata (Orthoceras) is not the internal position of the shell or the associated acquisition of secondary shell parts, but the marked reduction of the ventral shell margin together with the adjacent primary or skin mantle. The organs of the mantle cavity would be freely exposed, were it not for a new structure, the muscular mantle (p. 93), which replaces the missing parts. Thus, the shell of Protodibranchus differs from that of Orthoceras not only in the presence of a periostracum, but also in the absence of a ventral delimitation of the living chamber the dorsal part of which is preserved as a spatulate process of the wall of the conical chambered region. The parts are called, like in the belemnites: proostracum — the dorsal part; phragmocone — the chambered section, i. e. the series of chambers; conotheca — the wall of the phragmocone. The septa are watchglass-shaped and convex posteriorly, produced into typical septal necks, and with the siphuncle situated closely to the ventral margin of the septa. The phragmocone is completely calcified, while the anterior and marginal parts of the proostracum are soft and elastic, consisting only of conchiolin. The posterior parts, however, are probably more or less calcified. As is usual in molluscs, the characteristic form of the shell margin is reflected in the growth lines, which show the relationships known from the belemnites and permit a reconstruction of the whole from a few fragments, particularly of the proostracum, which is usually missing.* The belemnites, however, are typical decapods (Chapter 3) and far more specialized than Protodibranchus, although they retain some shell characteristics of the latter. There is no reason to assume that the common ancestors of Octopoda and Decapoda already had a characteristic, belemnite-like rostrum as a differentiated part of the periostracum. The corresponding element in these early forms is the posterior end of the shell, which may be assumed to have been more or less pointed.

93 The muscular mantle is an important organ in the Dibranchiata, consisting of a thick plate which replaces the living chamber and consists of crossed muscular systems — mainly radial and circular. This took place gradually in the course of evolution, in the degree the living chamber became incomplete by recession of the ventral margin of the shell (Figure 24). The muscle mantle is inserted primarily at the shell margin, i. e. ventrally, at the edge of the conotheca and dorsally at the proostracum. Physiologically and ecologically the muscular mantle is mainly an organ of movement the rhythmic contractions of which widen and contract the mantle cavity (p. 83). During "diastole," water enters along the mantle margin and is expelled through the funnel during the "systole." The funnel apparatus thus becomes a more passive organ of movement, without completely losing its own contractions. The cephalopodial retractors also participate in locomotion; rhythmic retraction of the entire cephalopodium can be observed in many

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* What applies to the Decapoda about the structure of the proostracum, its division into middle and lateral plates and the occurrence of asymptote lines (Figures 34 and 47, Chapter 3) may also apply here. This cannot be definitely determined, however, since the rudimentary shells of the Octopoda make comparison impossible (pp. 13 and 32).

swimming Dibranchiata, the effect being enhanced by the development of powerful funnel retractors (pp. 86 and 99).

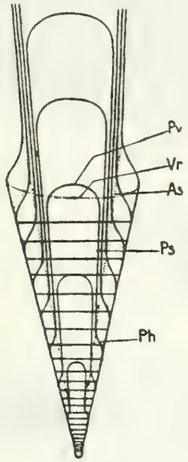

FIGURE 24. Phragmocone and posterior part of the proostracum of a typical dibranchiate (belemnite), diagrammatic, dorsal view. The growth lines curve into the proostracum, forming asymptotes which lie between the longitudinal growth lines on the phragmocone [not in figure] and cut a wedge out of the conotheca. If the proostracum is absent, its form can be determined from the growth lines in this zone:

Ph — phragmocone; Ps — proostracum of a young stage; Pv — its anterior margin; As — asymptote; Vr — ventral margin of the conotheca (covered).

The possible origin of the muscular mantle is shown in Figure 22. It is evident from the transitional stage illustrated that the muscular mantle is the modified free margin of the primary or skin mantle. Since the muscular mantle occupies topographically the position of the skin mantle, it could be assumed to be homologous to it, i. e. a modified skin mantle. This, however, is not the case (Naef 1913, Figure 26). Since the ventral shell margin of Dibranchiata (with a developed shell) is homologous to that of the Tetrabranchiata, it follows that the outer boundary of the primary mantle (i. e. the shell epithelium) of Protodibranchus is situated in the wall of the shell sac. This can be clearly understood by careful comparison of Figures 19 and 23 (see also Figure 9). The inner boundary, however, is apparently displaced, at least partly, to the skin of the abdominal complex,
94 which is suggested by the position of the nidamental glands. The morphological position* of the inner boundary is situated in the Dibranchiata at the exit of the posterior pallial veins from the renal sac (Figure 35). In Nautilus this is situated at the beginning of the mantle (Figure 20; cf. Naef, 1913), so that the nidamental glands are situated entirely on the mantle. In the Dibranchiata, however, it is displaced to the anal complex. Thus, it is not inconceivable that the nidamental glands have also taken part in this shift. At any rate, their position must be considered as homologous to to the part of the inner mantle skin to which they are attached in Nautilus, the transfer being associated with the rudimentation of the primary mantle.

The muscular mantle is thus a new formation in the Dibranchiata. It develops from the outer margin of the primary or skin mantle, which has become rudimentary together with the adjoining shell area and its remnants are found in different places.

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* The "morphological position" is the topographical relationship to the primarily adjacent organs. It is not necessarily changed if an entire complex is transferred, although in that case the actual "position" occupied will be different.

In Protodibranchus remnants of the primary mantle are also found in other places, namely wherever the shell extends from the back above the mantle cavity. This applies especially to the anterior part of the proostracum below which the mantle cavity extends far e.g. near the collar (Figures 19 and 23), as well as to a few marginal parts of the proostracum which project above the attachment of the soft parts, e. g. behind the gills (Figure 33, Mp; cf. Loligo).

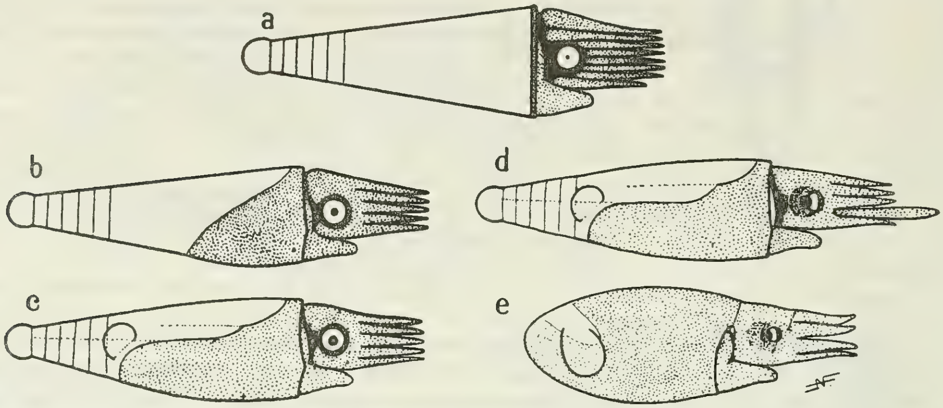

FIGURE 25. General orientation of the phylogeny of Dibranchiata. Five ideal (hypothetical) young stages are shown:

a — Orthoceras; b — transitional form; c — Protodibranchus; d — Protodecapus; e — Protoctopus. The scheme illustrates the modification of the arm series; the formation of the orbit and primary eyelid, which is assumed to be still wide open in Protodibranchus. Most important are the development of the muscular mantle from the margin of the primary mantle and the gradual reduction of the shell by this organ, which is most extreme in the Octopoda.

95 The free margin of the muscular mantle bears ventrally a shallow, wide incision for the funnel, while laterally there is a smaller incision for the funnel pockets. This close contact with the funnel apparatus is probably an important factor in the development of the muscular mantle. Even before the mantle cavity is constricted to an appreciable extent (Figure 20b), the muscular mantle would have assisted the function of the funnel by improving the closure of the mantle slit and would have strengthened the contraction of the funnel, which can be achieved directly by active narrowing of the mantle opening or indirectly by the resulting powerful contraction of the funnel apparatus itself. Protodibranchus has a pair of small, round fins, which are attached on the outside of the shell between the conotheca and proostracum (Figure 23). Because of their articulation with the shell, the fins can be slightly moved in a horizontal and vertical direction (Figure 25). The fins are attached to the smooth shell epithelium, which is reinforced by a cartilaginous layer, so that a kind of articulated capsule

is formed by the adjacent part of the shell sac. The base of the fin is moved by specialized skin muscles and glides back and forth on the articulation surface provided by the shell.* Alternating contractions of an upper and a lower layer of transverse (vertical) muscles draw the fins up and down, helping to maintain equilibrium. The fins are differentiations of the shell fold, as their development shows (Volume II); their primary place (morphological position) is that part of the outer side of the shell where the proostracum passes into the conotheca. The branches of the posterior pallial vein, which supply the fins, enter the shell fold at this point.

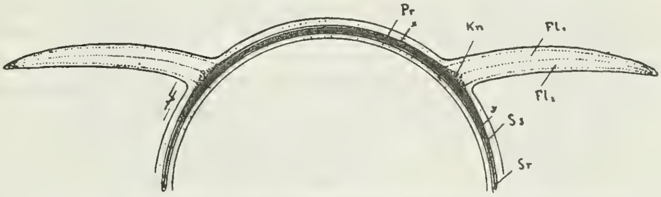

FIGURE 26. Diagrammatic cross section of the posterior part of the body of Protodibranchus at the junction of proostracum and conotheca. (Compare Figure 41, according to which this scheme should be completed.) The fin cartilage which strengthens the fin base is connected with the outer epithelium of the shell sac. This epithelium glides on the shell between x and y. (In the higher Dibranchiata a corresponding area becomes detached from the rest of the shell sac during the embryogenesis; q.v.):

Sr — shell margin; Ss — shell sac; Fl_1 and Fl_2 — fin muscles; Kn — fin cartilage; Pr — proostracum.

The eyes are very large, situated laterally on the head and directed
slightly forward, and are much more advanced than those of Nautilus
(and Protorthoceras). The eye chamber is closed and the margins of
96 the primary eyecup fused into a double epithelial lamella ("corpus epi-
theliale") which produces and bears the lens (Figure 27). The lens is
spherical and consists of two unequal parts (Figure 28), of which the outer
is smaller and develops later. Both parts are separated by the corpus
epitheliale, the adjacent layers of which secrete the corresponding lens.
Around the outer lens segment develops the iris, a circular fold which
adheres to the lens and forms a secondary pupil. The iris fold is not of
equal width all around; its upper margin is enlarged, blinkerlike, while the
lower margin slightly projects, forming a bean-shaped pupil (Figure 52).
The iris, however, is highly contractile, and can markedly constrict or
97 widen the pupil. The eye projects from its attached base (Figures 27 and 28),
and is situated in a deep pocket, above which is a circular fold with an
opening of moderate size. The margins of this opening are equipped with
a circular musculature which can reduce it to a small hole to protect the
organ. This translucent primary lid fold is transparent above the lens,
and little affects visual acuity.

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* For the justification of this assumption, see Chapter 3 and the description of the development in Volume II of Part 1 and in Part 2 of this work.

Behind the eye there is a round, flat papilla, the "olfactory organ" (see p. 82).

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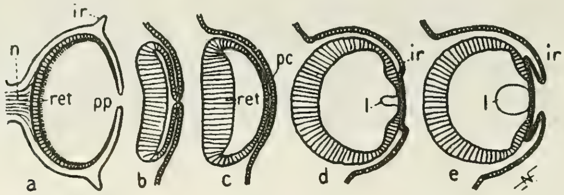

FIGURE 27. Diagrammatic frontal sections of the development of the right eye of Cephalopoda:

a — Nautilus. The stalk bears the optic nerve (n); the retina (ret) is actually many-layered with the rods pointed toward the light; other elements are the primary pupil (pp) and the ring fold (ir) which forms a wide circle and probably corresponds to the iris of Dibranchiata; b — e — typical stages of the embryonic eye of Sepia. The eye chamber is completely closed. The double epithelial lamella (pc), which becomes thinner later, forms the lens (l) at the site of the primary pupil; only the inner segment of the lens is formed at first. (Compare description of development in Volume II.) Close around the lens develops the iris fold (ir). The resulting eyeball (e) is comparable to that of Nautilus in the following aspects: it projects from the head, and is borne in the embryo on a more or less distinct stalk which is much thicker here because the organs it contains are more developed than those of Nautilus (optic ganglion, white body; see Figure 28).

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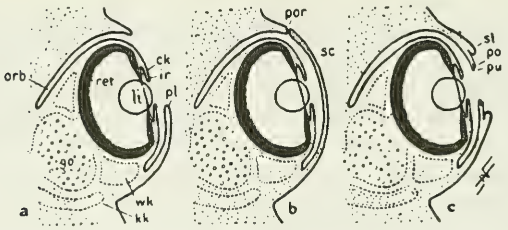

FIGURE 28. Frontal sections through the right eye of different Dibranchiata (diagrammatic). a) Typical form, found in Oegopsida. The orbit (orb) is wide open; the posterior margin (pl) of the orbital opening forms a primary lid which can cover the lens. This protective closure becomes permanent in Loligo (b), in which the primary lid fold develops into a cornea (sc) and the communication of the orbit with the exterior is reduced to a narrow pore (por). In Octopoda (c) (q.v.) the primary lid margin becomes complicated and a secondary lid fold appears at its periphery:

go — optic ganglion; wk — white body; po — primary upper margin of the primary lid; pu — primary lower margin of the primary lid, overlapping in Octopoda.

The protective envelope of the eye, i. e. the wall of the eye socket and the primary lid fold, are derived from the arms. This is evident from a comparison with Nautilus (Figure 7) or Protorthoceras (Figure 19), in which the eye is surrounded by a number of arm bases or "arm pillars" which project elbowlike to the outside (p. 61). Another proof can be found in the embryogenesis of the Dibranchiata (see Volume II); the eye is first surrounded by differentiated arm pillars which later become fused into a closed wall-like structure – the primary lid fold (Figure 33b shows these states in the Tetrabranchiata). The margins of the arm pillars face the eye from above, in front and below, from which the primary lid margin mainly develops; they are joined posteriorly by a skin fold which develops from the skin of the head and connects the free posterior ends of these margins. This skin fold separates the eye from the olfactory organ, so that it is situated outside the orbit, in contrast to the condition in Nautilus in which the organ is situated inside the eye socket, which is therefore only partly homologous (Figures 7 and 19, p. 61). In connection with the formation of the primary lid, the other parts of the arm pillars also become fused (Volume II) into a uniform cephalic sheath (p. 65) which in the adult forms the muscular subcutaneous layer of the head and does not show that it consists of parts of the individual arms (Figure 33a).

The head of Protodibranchus bears an outer circle of at least 10 strong outer arms of more or less similar structure and length. Each of these arms bears a row of cup-shaped suckers which become gradually larger from the base, but become smaller toward the apex until they become invisible to the naked eye. On each side of the suckers there is a row of small, movable processes or palps which alternate regularly with the suckers, so that they form pairs (Figure 12). The arms are more or less quadrangular in cross section with one outer, one inner and two lateral surfaces. The inner surface is delimited by the rows of palps. The arms are connected by the interbrachial membranes attached to the margin of the outer surface of the arm, and bear a marginal muscular cord extending in the outer margin toward the apex of the arms. Spreading of the arms and contraction of the marginal muscles expand the skin folds into a large umbrella which closes like a sac around the prey. The secretion of the
98 poison glands is released into this narrow space, rapidly paralyzing the captured animal.

The suckers of Protodibranchus are assumed to be similar to those of Octopoda, the simple structure of which undoubtedly has to be considered as a primitive character (Figure 29, Plate XIII). They are not attached directly to the inner surface of the arm, but are situated on a movable stalk which gives them a greater field of action. Viewed from above, they are circular; the opening leading to the suction chamber is surrounded by two zones — an inner grasping ring and a marginal ring. The marginal ring is soft and adheres immediately to the objects touched; the grasping ring is strong, with fine radial grooves and projects near the opening in a blunt edge. The suction chamber widens slightly towards the base where it is thicker (suction pad). The suction chamber (with the suction pad and wall ring) and the grasping ring are equipped with powerful muscular walls with predominantly radial fibers, the contraction of which widens the cavity and stiffens the walls. During the sucking, the funnel-shaped grasping ring adheres completely to the object, bringing it in contact with the chamber margin.

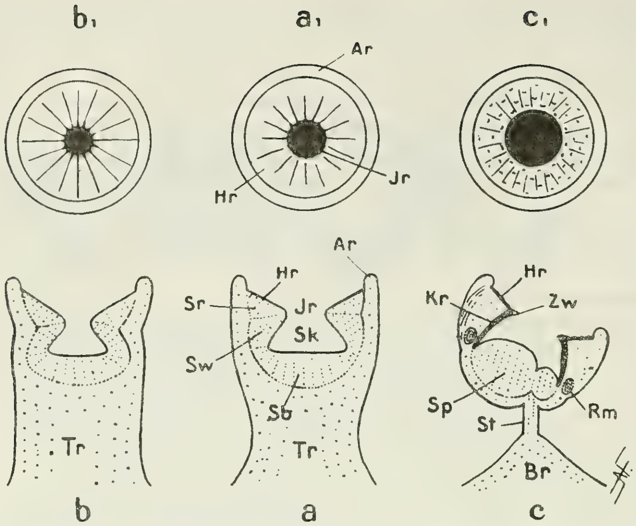

FIGURE 29. Morphology of the suckers of Dibranchiata. Median section (below) and upper view (above) of typical suckers of Protodibranchus (a), Protodecapus (b) and Protoctopus (c):

Ar — marginal ring; Hr — grasping ring; Jr — chamber margin; Tr — support; Sr — muscular wall layer of the grasping ring; Sw — muscular layer of the side wall; Sb — muscular layer of the chamber bottom; Sp — sucking pad; St — stalk; Br — basal pad; Rm — circular muscle; Kr — chitinous chamber ring; Zw — chitinous teeth on the chamber margin.

[There is apparently a mistake in the labeling in Figure 29: b and c are interchanged. Compare Figure 389, p.662 of the structure of the suckers of Octopoda and Decapoda.]

The marginal ring becomes active mainly during the capture of prey, providing a first, slight adhesion; later it perhaps prevents the entry of water between the object and the grasping ring. Detachment of the sucker is effected by special circular fibers near the sucker.

99 Inside the outer series of arms there is a series of oral arms, which consists of at least 8 arms the suckers of which are much smaller than those of the outer arms, almost rudimentary. The oral arms are also webbed at the base by skin folds which enfold the prey while the jaws, poison glands and radula are activated. I use the following terms for these parts: buccal membranes for the skin folds, buccal pillars for the oral arms, and buccal funnel for the entire series of arms.

As in the Tetrabranchiata, the mouth is delimited by the outer and the inner lip. The jaws may project and extend forward from the inner lip, like the radula when the lip opens. The jaws of Protodibranchus differ from those of Nautilus mainly in being more delicate; this is true of the outer and inner plates as well as of their end and the biting edges. The apex of the jaws consists entirely of a chitinlike substance, without a calcareous coat. The lateral wings of the lower jaw (Figure 30, Ap) are much narrower than the jaws of the known fossils and recent Tetrabranchiata, and their inner plate extends posteriorly far beyond the margin of the outer plate, forming a blunt median edge and a short open groove. The inner plate of the upper jaw forms a narrow arch.

The radula follows the pattern of Tetrabranchiata with the following exceptions. The number of teeth in each transverse row is reduced from 13 to 9 (Figure 14); the 3 median teeth of each row (rasping teeth) are more complicated in having 1 or 2 smaller cusps in addition to the main cusp. The following rows of teeth remain after the intercalary and paramedian rows (p. 67) have disappeared: one row of marginal platelets on each side, two lateral rows of brush teeth on each side, one submedian row of rasping teeth, and one median row of rasping teeth. Figure 31 shows a complete radula, although not of a typical character in some details.

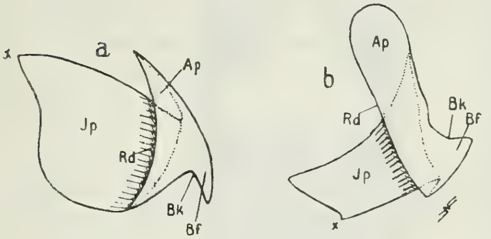

FIGURE 30. Profile of typical jaws of Protodibranchus. The upper jaw (a) does not differ markedly from that of Nautilus (Figure 13). The lower jaw (b) consists of a large inner plate (Jp) and an outer plate (Ap) with rather narrow lateral wings:

Bk — biting edge; Bf — biting process; Rd — posterior margin of outer plate.

As in the Tetrabranchiata, the funnel apparatus consists of a collar, funnel pockets and a funnel tube. The latter, however, is not conical as in Nautilus and Protorthoceras.
100 Instead of overlapping as in these two forms, the two funnel lobes are fused in the median plane to form a tube. This reduces the expansion of the inner space so that its role is more passive (p. 84). This is compensated by the muscular mantle, which can expand and contract the mantle cavity and increases the stability of the whole mechanism. The funnel retractors (Figure 35, Rt) have the same effect. They are much more developed, they are united posteriorly with the cephalopodial retractors and reach the shell at the transition between proostracum and conotheca at a
102 point corresponding to Sp in Figure 34. At the origin of the retractors, i. e. at the site of the funnel septum, the posterior margin of the funnel forms the funnel corners (Figure 35, Te). These corners extend posteriorly; they are slightly curved ventrally and form shallow depressions on the mantle which also contribute to the stabilization of the locomotory mechanism.

The funnel gland (or organ) is situated in the funnel. This organ consists of 3 large areas of modified, padlike raised epithelium which form together a large mucous gland. Figure 23 shows a section of the upper median epithelial area. From this point, the epithelium projects posteriorly in two branches on each side toward the inner opening of the funnel; the two other areas are situated laterally in the form of oval pads extending from the lateral to the ventral part of the funnel (Plate VII, Figure 2).

The organs of the mantle cavity of Dibranchiata are best studied in their natural position by removing the whole ventral part of the muscular mantle. Figure 33 (35) shows this operation in the case of Protodibranchus. The muscular mantle is removed posteriorly to its insertion at the margin of the conotheca, while the areas attached laterally to the proostracum remain intact.

There are only two gills. Comparison of Figures 20 and 33 shows that the upper (anterior) gills of Nautilus, in which they are already smaller, have disappeared. The remaining pair, i. e. the lower (posterior) gills (see p. 84) are relatively enlarged, however, and differ from those of the

the Tetrabranchiata in the following points: 1) the formation of a well-defined branchial gland in their axis, and 2) the stronger development of the branchial ligament, which extends to the apex of the gill and connects it with the mantle in the greater part of its length. A pocketlike structure, the gill root pocket, is situated above the gill base between the gills, mantle, the abdominal part of the body and the infundibular retractor.

(100)

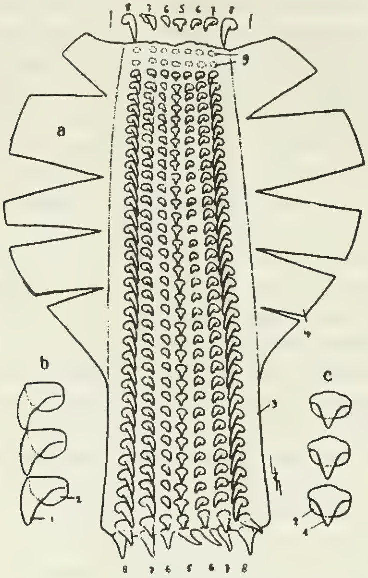

FIGURE 31. Radula of Sepia orbignyana (10×). The radula has been detached from the tongue by maceration and then spread and dried on a slide (this is the only method of obtaining good preparations). The main plate (3) is flanked anteriorly by the lateral plates (4) which must be cut before spreading since they are curved over the tongue process (Figure 23) the sides of which are occupied by the lateral plates. 5 – 8 – teeth on main plate; c – some teeth of the median row; b – teeth of the second lateral row of the right side with basal plate (2) and dental process (1). The 7 rows of teeth contain median rasping teeth (5), submedian rasping teeth (6), and inner (7) and outer (8) brush teeth. (Sepioidea lack the marginal platelets shown in Figure 14.) Scars of fallen teeth in the recurved distal part of the radula are visible at 9 (Figure 23). At the opposite end, there are soft new teeth. The figure does not show exactly the typical condition, at least with respect to the specific formation of the teeth rows. The general arrangement, however, corresponds to the nearly constant typical condition in the Dibranchiata.

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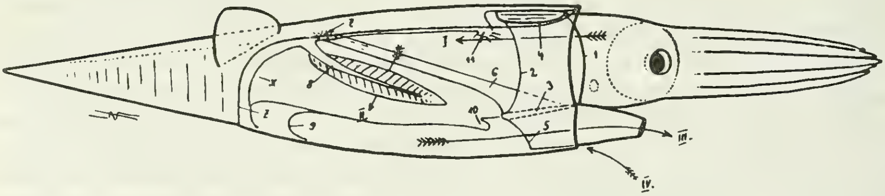

FIGURE 32. Diagram of the swimming and breathing mechanism in the Dibranchiata. The arrows show the path of the water current during pulsations of the mantle: ingress ventrally between the funnel and mantle margin (IV), laterally between the funnel pockets and mantle (I), passage from the laterodorsal to the ventral part of the mantle cavity median to the gills, washing them (II), egress through the funnel (III):

1 – anterior margin of funnel pocket; 2 – posterior margin of funnel pocket; 3 – funnel part adhering to the mantle; 4 – collar; 5 – posterior margin of the funnel; 6 – funnel retractor; 7 – origin of the retractor on the shell; 8 – gill; 9 – anterior margin of the mantle septum; 10 – anal papilla; x – bottom of the mantle cavity; z – margin of the conotheca (attachment of the muscular mantle).

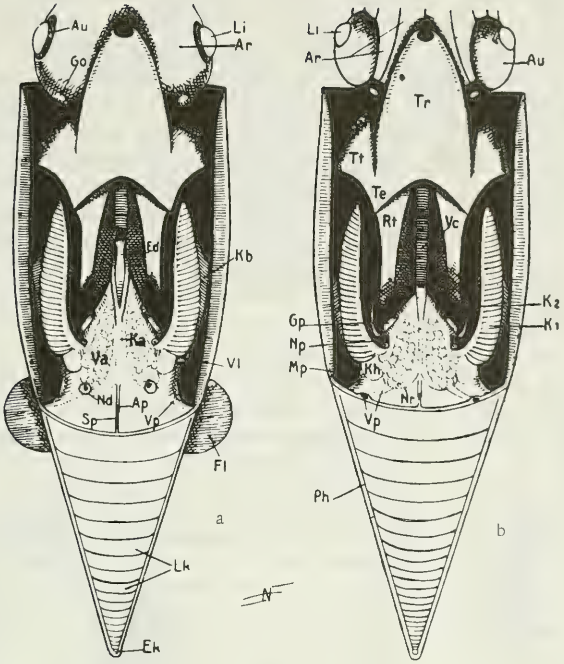

FIGURE 33. Morphology of the mantle cavity situs in the Dibranchiata. a) Form in Protodibranchus in a normal position, after removal of the ventral part of the muscular mantle. The round head bears open primary lids and prominent eye lenses, as well as an oval olfactory tubercle (Go). The funnel apparatus consists of funnel and funnel pockets. The funnel retractors originate at the funnel septum which divides them and continue toward the lateral margin of the shell. The gills are attached (Kb) to the mantle. Also shown are the kidneys and the genital papillae at their root; the course of the vena cava and the position of the characteristic anal papilla (Ed); the position of the renal sacs with the translucent venous appendages (Va); the course of the musculus rectus abdominis (Ka), the posterior pallial veins (Vp) and the posterior pallial artery (Ap); the position of the branchial hearts and the lateral pallial vein (Vl); the formation of a median pallial septum (Sp) by the shortened connection of the posterior pallial artery with the muscular mantle. b) Diagram for explanation of (a) and for comparison with the Tetrabranchiata (Figure 20). A rudimentary upper (anterior) gill (K_2) is shown. The anus is still in a transitional position, like the posterior pallial artery and veins. Fins are still absent. On the head, the orbit is still incomplete, a true lid is not yet developed, although the arm pillars (Ar) are beginning to form a lid. Such a transitional form ("Praedibranchus") cannot be constructed reliably since we do not know the actual sequence of changes leading from Orthoceras to Protodibranchus, and the figure should be considered only as instructive, like Figure 20b. It is very doubtful that the different transitional characters all appeared at the same time.

Au – eye; Go – olfactory organ; Li – lens; Ar – arm bases, more or less fused into a cephalic sheath (p.65); Tr – funnel; Tt – funnel pockets; Te – funnel corners; Rt – infundibular (funnel) retractor; Vc – vena cava; Ed – intestine; Ka – musculus rectus abdominis; Va – vein appendages; Nd – rudimentary nidamental glands; Ap – median pallial artery; Sp – mantle septum; Vp – posterior pallial vein; Fl – fins; Vl – lateral pallial vein; Kb – gill ligament; Lk – air chambers; Ek – embryonic chamber (not shown in the drawing on the right); Ph – phragmocone; Nr – margin of the renal sac; Kh – branchial heart; Mo – remnant of the primary mantle; Np – renal papilla; Gp – genital papilla; K_1 – ventral gill; K_2 – dorsal gill (lacking in Dibranchiata).

As in Nautilus (see p. 70), the renal papilla of the posterior kidney is situated before the basal swelling of the efferent branchial vessel. The anterior papilla has disappeared together with the kidney, but the papilla has persisted and continues to discharge the genital products. In the mature animal, it grows to a large, projecting "genital process"* which develops deep inside the gill root pocket but later grows toward the anus (Figure 35). The anus is displaced far toward the inner opening of the funnel on the vena cava. In the Dibranchiata, it consists of a strongly projecting papilla with a terminal swelling which opens in a transverse slit; around the papilla are situated 4 elevations or anal lobules — one dorsal and one ventral — both lip-shaped, and two leaflike lateral lobules with keeled outer sides. The entire stereotypic structure will be referred to later as the anal papilla for simplicity.

(104)

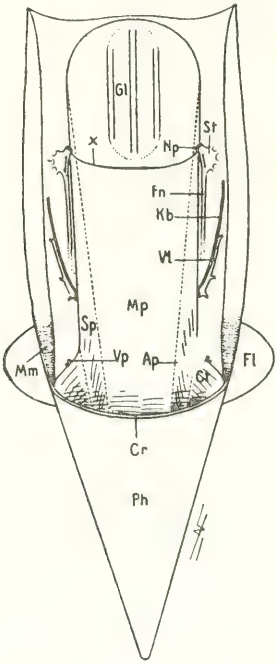

FIGURE 34. Morphology of the shell situs in the Dibranchiata (emptied mantle sace of Protodibranchus). The figure shows relationships which appear after the removal of the viscera in the imaginary preparation illustrated in Figure 33. The shell is freed of the soft parts which occupied its cavity. The anterior end of the proostracum, however, is covered by the mantle insofar as the mantle cavity extends to this place, i.e. as far as the line connecting the two stellar ganglia (x). The adhesion and gliding surface opposite the collar is stressed (Gl). Important aspects are the attachment of the muscular mantle to the proostracum and the transition of this attachment to the margin of the conotheca (at Vp); the entry of the posterior pallial artery (Ap) and posterior pallial vein (Vp) into the muscular mantle (towards the fin); the course of the lateral pallial vein (Vl) and the position of the stellar ganglia (St):

Gl — collar; x — posterior border of the dorsal mantle cavity; Np — entrance of the pallial nerve; St — stellar ganglia; Fn — fin nerve; Kb — gill ligament; Vl — lateral pallial vein; Mp — median plate of the proostracum; Sp — lateral plate of same (Chapter 3); Mm — muscular mantle; Vp — posterior pallial vein; Ap — posterior pallial artery. (Reference line is defective, like the adjacent part of the figure, which should be completed as on the left.); Ct — conotheca; Fl — fin; Cr — margin of conotheca; Ph — phragmocone (Figure 24).

103 A very characteristic structure of the Dibranchiata is the ink sac, which was absent in the Tetrabranchiata, as far as we know. It is situated above and only partly covered by the intestine (Figure 37, Ed), which passes close to the surface in the anal area. The ink sac is usually visible through the skin (Figures 35 and 47); at first it is strictly symmetrical with the piriform end posteriorly. The ink sac discharges dorsally into the intestine near the anus.

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* I have found no better term for the projecting terminal parts of both sexes, which in the male usually bear the incorrect name "penis." This term is as unsuitable as that for the female organ, which is often quite similar. Both organs are used for the transfer of the genital products (eggs, spermatophores) to the funnel opening or hectocotylus.

A delicate superficial muscle (musculus rectus abdominis) passes in the median line in the area between the renal papillae, branches anteriorly around the anal papilla (cf. Octopoda and Sepiolidae) and ends posteriorly near the emerging posterior pallial artery. On either side of this muscle are situated the renal sacs with the translucent venous appendages. These meet beneath the skin, forming a double septum. The posterior pallial artery emerges between their posterior parts; it does not extend to the origin of the muscular mantle at the margin of the conotheca but passes in the margin of a fold, the median pallial septum, directly to the muscular mantle. (In the drawing the artery has been cut off where it reaches the mantle.) The two large posterior pallial veins emerge at the posterior margin of each renal sac from the shell fold and the mantle where the proostracum is fused with the conotheca. Part of their blood comes from the fins, which are situated outside this point (Figure 34). The branchial hearts are visible at the lateral margin of the renal sacs near the gill base. The lateral pallial vein passes on each side of the base of the gills and continues along the attachment of the gill ligament to the mantle.

(105)

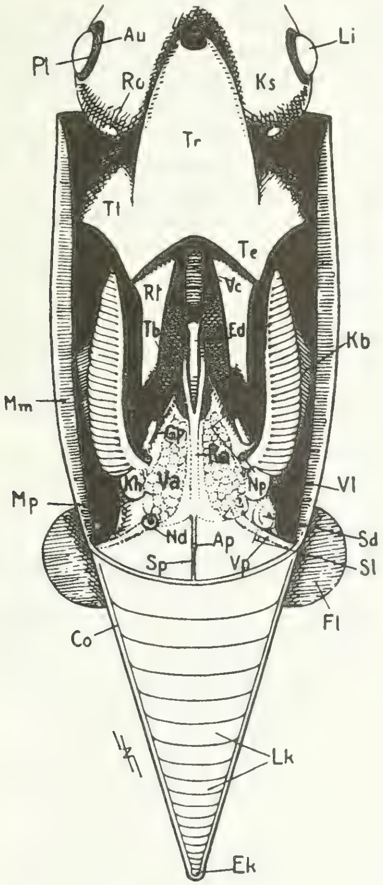

FIGURE 35. Morphology of the mantle situs in Dibranchiata. Female characters are shown on the left, male characters on the right. Compare with Figure 33, with particular attention to the different form of the genital process (Gp) in the male and female (right and left). The male organ projects from the opening of the genital pocket, which extends far posteriorly and surrounds the spermatophore gland (translucent through the skin):

Sl – primary sperm duct, showing how far back the original genital opening has been displaced; Au – eyeball; Pl – primary lid; Ro – olfactory organ; Ks – cephalic sheath; Li – lens; Tr – funnel; Tt – funnel pocket; Te – funnel corner; Rt – funnel retractor; Vc – vena cava; Ed – intestine; Gp – genital papilla; R – musculus rectus abdominis; Va – venous appendages; Kh – branchial heart; Np – renal pore; Nd – nidamental gland; Ap – median pallial vein; Sp – mantle septum; Vp – posterior pallial vein; Mm – muscular mantle; Mp – primary mantle; Co – conotheca; Ek – embryonic chamber; Lk – air chambers; Fl – fins; Sl – sperm duct; Sd – spermatophore gland; Vl – lateral pallial vein; Kb – branchial attachment.

Figures 15, 20 and 30 permit a closer comparison of the mantle cavity of Dibranchiata and Tetrabranchiata. The abdominal complex of Nautilus (p. 70) can be easily recognized in them. In the Dibranchiata, this complex is situated behind what is here the anterior mantle groove. The latter, corresponding to the upper mantle groove of Nautilus, cuts in above the anal papilla, which it detaches from the body, and extends toward the gill roots. (This complex consists of the renal pores, the renal sacs with the translucent venous appendages, the gills and the vessels which enter into the mantle, i. e. the median pallial artery and the posterior pallial veins.) The groove is completely homologous to that in which the genital openings are situated in Nautilus (Figure 16). Except for the laterally folded gills, Figure 15 is directly comparable with Figure 33a, and the following conclusions can be made: the renal papillae of Dibranchiata replace the lower papillae of Nautilus together with the pericardial funnels, while the genital papillae (genital processes) correspond to the upper papillae together with the genital openings.

The anterior kidneys and gills in the Dibranchiata would also have been associated with the genital openings in their primary position, if they had been present as rudiments, which is not the case (Naef, 1917, p. 59).

A characteristic new development inside the mantle cavity are the stellate ganglia of the Dibranchiata. Ontogenetically, the stellate ganglia are differentiations of the inner side of the muscular mantle and should, therefore, be regarded in connection with it. The stellate ganglia are absent in Nautilus. They innervate mainly the muscular mantle, chromatophores,
104 and fins — structures specific for the Dibranchiata and absent in the Tetrabranchiata. They have some topographical relationships to the gill base (cf. Volume II). The stellate ganglia are flat elevations of the inner side of the mantle with nerves radiating from them in the form of ridgelike processes. The ganglia are situated on each side of the proostracum at the origin of the muscular mantle, at about the same distance from the mantle margin as the mantle cavity enters mediodorsally (Figure 23). To expose the ganglia, it is necessary to remove the gill ends, although their topographical relationships are best recognized by emptying the shell cavity and detaching the gills and vessels from the mantle.

Figure 34 shows the primary topographical relationships between the shell, muscular mantle, the remnants of the skin mantle, stellate ganglia, collar, insertion of the gill ligaments and the entrance of the pallial veins. They are markedly changed in all recent forms, but the relationships illustrated provide the necessary basis for the morphological understanding of these variations.

There is an important difference in the development of the outer genital openings, in spite of their misleading similarity in Figure 33. This difference results from the embryonic development and will be outlined briefly. In both sexes, as in Nautilus, a glandular ectodermal invagination is connected with the mesodermal gonoduct, so that its primary opening is displaced to a deeper position. In the female, however, the opening of the
105 glandular terminal region (oviduct gland) appears on the apex of a developing genital papilla as a secondary orifice, while in the male it becomes the opening of the genital pocket (Naef, 1913, pp. 444—447) — a sac which at first opens at the same place and inside which the spermatophore glands and sperm duct are formed by a process of constriction. The end of the

sperm duct grows out of the genital pocket in the form of a papilla and forms a tertiary outlet of the genital organs, resembling, but naturally not homologous to, the secondary opening of the female or to the tertiary opening in Nautilus (p. 72). The homologue of the female genital opening in the male is actually the wide opening of the genital pocket which envelops the projecting genital process like a foreskin (often named "penis"). This is shown in Figure 35.

When the outlet of the genital pocket is closed, it adheres so closely to the projecting genital process of the male that no open slit is visible. This is a preparation for the state in most Loliginidae, Sepioidea and Octopoda, in which the slit is closed by fusion with the genital process.

106 We assume that the female Protodibranchus had typical nidamental and accessory glands similar to those of Decapoda (q. v.) or with some primary primitive characters as in Nautilus, although there is no evidence for this. Of all forms derived from Protodibranchus, only the Decapoda have nidamental and accessory glands, while the Octopoda show no trace of them (no longer). The assumption that these organs existed in Protodibranchus is based on their undoubted presence in Nautilus. We know nothing about them in Protorthoceras (p. 86), or about their development ("metamorphosis") from Protodibranchus to the Decapoda. Only the position of the nidamental glands must have corresponded to that observed in Decapoda, as their displacement is connected with the dibranchiate character, i. e. the formation of the muscular mantle and the reduction of the ventral part of the shell which distinguishes Protodibranchus from the Tetrabranchiata (cf. p. 93). Thus, the "anlage" of the nidamental glands occupies the position shown in Figure 33, the accessory glands some distance further anteriorly, closer to the median plane (Plate II, Figure 2).

Protodibranchus is assumed to show a typical external sexual dimorphism which develops only at the time of maturity. In the female, the entire posterior part of the body becomes relatively longer and much thicker than in the male, owing to the marked enlargement of the ovary. This is often evident from the shell, which becomes wider than in the male. In the male, all arms become stronger (hectocotylization) including the basal musculature of all arms, so that the whole head part becomes larger; another difference is the enlargement of the suckers, particularly in the proximal third (cf. the chapters on Illex and Loligo). During copulation, the female is held firmly with the arms and one arm, the hectocotylus, transfers the spermatophores to a certain place below the mouth, where they are discharged and attached. From the spermatophores oozes the semen which fertilizes the eggs during the oviposition when the egg mass is formed and deposited by the arms. One or several arms may show particular adaptations for the transfer of eggs. Such modifications, however, cannot be important in the ancestral form, since no generally valid characterization of them can be given for the Dibranchiata.

c. TYPICAL POSTEMBRYONIC DEVELOPMENT

While the typical postembryonic development of the Cephalopoda in general, i. e. of the Tetrabranchiata, was briefly outlined in the first chapter and will be completed in Volume II on the basis of data from the embryonic period, the typical ontogenesis of Dibranchiata can be characterized on the basis of extensive comparison. (Volume II deals with the early stages until hatching.)

107 The older embryos (Figure 36) still have a rapidly decreasing external yolk sac the envelope of which hangs like a hernia of the body wall below the mouth between the outer lip and the buccal margin. When the yolk is resorbed, the sac disappears and forms a small area of ordinary skin. This indicates hatching. The newly hatched animal resembles the adult in characters like the internal shell, shell sac, muscular mantle, fins, funnel apparatus, eye, arms, etc. Young Dibranchiata are not larvae, even if they show marked differences from the mature form in special cases.

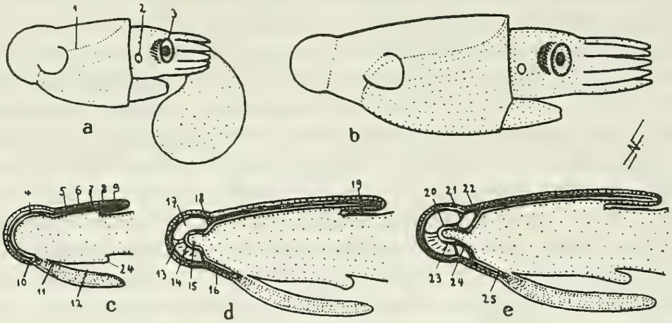

FIGURE 36. Embryos of Protodibranchus:

a – young embryo; b – older embryo (magnified about 6×; c – median section through stage (a); d – median section through stage (b); e – median section through an older animal; 1 – origin of the muscular mantle on the shell margin; 2 – olfactory organ; 3 – primary lid; 4 – primordial shell; 5 – shell fold; 6 – proostracum; 7 – secondary shell epithelium; 8 – primary shell epithelium; 9 – primary mantle; 10 – ventral margin of the embryonic shell with the beginning of the muscular mantle (11); 12 – mantle cavity; 13 – prosiphuncle; 14 – initial caecum; 15 – siphon; 16 – conotheca; 17 – embryonic chamber; 18 – first septum; 19 – collar; 20 – siphuncle; 21 – first septum; 22 – second septum; 23 – initial caecum or first septal neck; 24 – second septal neck; 25 – ventral margin of the conotheca with the insertion of the muscular mantle; 24 (in c only) – anal papilla.

Some organs appear to be less differentiated. The number of chromatophores is still very small (compare with Ctenopteryx, for example). The arms are still very short, with a small number of developed suckers, and with new suckers being continuously added at the distal end of the row (Plate X). The end of the arm functions as a vegetative center with embryonic tissue, like the apex of a cormophyte shoot, producing new parts as it grows (see Volume II). The palps of the arm are associated in pairs with each sucker. In the mantle cavity, the gills are similar, although they have at first only a small number of lamellae (cf. Loliginidae). The external genitalia are rudimentary or absent. The genital processes, accessory and nidamental glands are represented by thickenings of the epithelium; from the former develop almost the whole genital ducts (see Naef, 1913; cf. Chapter 3 about the development of the accessory and nidamental glands).

The determination of the primary relationships between animal and shell 108 and its formation is important. The conditions observed in the Dibranchiata give definite information on the first point. The muscular mantle of Dibranchiata always originates at the free margin of the embryonic shell or the corresponding point of the shell sac, which results from its derivation (Figures 20 and 25). Long before hatching, the shell is completely internal (in most Dibranchiata the shell sac is closed even before the shell develops). The shell appears at first as a free membrane consisting of conchiolin. It later becomes calcified, and forms two indistinctly separated areas — a scooplike, rounded terminal part which develops into the phragmocone, and a dorsally adjacent process which is the anlage of the proostracum. The primary shell epithelium is at first completely adjacent to the shell (Figure 36c) but later behaves as was assumed for Orthoceras (p. 88, Figure 22), producing successively the prosiphuncle, initial siphuncle, septal necks and shell septa. The secondary shell epithelium later also secretes shell substance (p. 92) forming a sheath which strengthens the delicate initial shell. This is all the more necessary because the shell is neither strengthened subsequently by thickening nor detached as in Orthoceras, and could have formed a vulnerable point of the organization.

The youngest stages always lack a sheath (as in Sepia and Spirula). Thus, the normal swimming position differs at first from the later horizontal position. The air content should raise the posterior end of the funnel, and its movement should resemble that observed in young stages of recent Dibranchiata (cf. Loliginidae).

d. VARIATION OF THE TYPE OF DIBRANCHIATA

The metamorphosis of the typical organization of Dibranchiata follows two directions represented by the orders Octopoda and Decapoda. Although these orders permit a methodical construction of their type and show numerous similarities, they differ sharply in many aspects, so that there can be no question of transitional forms between them. A characteristic contrast is the condition of the inner shell. In the typical Decapoda (Belemnoidea), the inner shell reached at first the conceivable peak of its development, and then underwent various modifications or even reduction. In the Octopoda, on the other hand, the development of an active muscular differentiation causes the loss of the passive-protective apparatus.

109 *Chapter 3*

ORDER DECAPODA
Leach, 1818

Contents: a. Diagnosis. – b. Typical structure of the adult animal. – c. Typical postembryonic development.– d. Variation of the type of Decapoda.

a. DIAGNOSIS

Dibranchiata (p. 90) with 10 outer arms, of which the fourth pair* (tentacles) is modified by lengthening of the basal part on which suckers are few or absent (forming a "stalk of the tentacle") and widening of the sucker-bearing terminal part into a "club." Suckers biserial or multiserial, with the opening protected by a horny ring which is often denticulate at the margin and may develop into a horny hook during postembryonic development. Normal suckers are separated by a deep constriction from their muscular support or basal pad, so that the connection is often only a thin stalk. Oral arms are still present as a distinct circle of 6—8 small rudiments connected by a skin fold — the buccal funnel. Renal pores more or less displaced from the gill roots toward the anus.** The funnel has a single valve (except in the Cranchiidae, q. v.) and is connected with the mantle on each side by an oblong, partly cartilaginous, cup-shaped disk (funnel cartilage) of varying form which resembles the collar in form and function.

b. TYPICAL STRUCTURE OF THE ADULT ANIMAL

The ancestral form of all recent and extinct Decapoda, which we named Protodecapus, combines all characters recognized as typical (primary, original) within the order. The picture obtained generally resembles that of Protodibranchus (p. 90).

The shell form and the general form of the mantle sac show no marked
110 differences from Protodibranchus. There is, however, a strengthening and differentiation of the sheath of the phragmocone or of the periostracum. These changes maintain the equilibrium of the air chambers and permit effortless swimming in a horizontal position. This function belongs to the sheath, since it strengthens the previously-formed delicate parts of the air-containing phragmocone and also adds to its weight. The type of typical

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* Counting from above.

** Cf. Naef, 1912, No. 11, p. 331.

growth displaces the center of gravity back, while the apex of the sheath (rostrum) becomes so massive that it appears as a separate formation from the rest of the secondary shell. As the phragmocone becomes longer anteriorly because of the marginal growth of the conotheca and formation of new air chambers, it can only be enveloped by the most recently formed sheath layer, while the previously formed layers are restricted to the posterior parts. The shell apex is thus covered by all layers and must be relatively the most weighted. This is also evident from the fact that the load of a given point depends on the circumference also if other conditions are equal, while the buoyancy is determined by the size of the cross section. As the phragmocone grows forward, the ratio changes in favor of buoyancy, the greater the distance from the posterior end. Thus, the Dibranchiata (p. 91) and, more specifically, the Decapoda have reached a hydrostatic adaptation to the hydrostatic conditions (further improved in the Teuthoidea and Sepioidea, q. v.). A further improvement is that the rostrum extends beyond the end of the phragmocone and becomes thicker apically. This is the case in various ancient types of Decapoda (Belemni-
111 tidae, Belopteridae and Spirulirostridae). The belemnites represent the simplest type, and the commonest form of their rostrum may be considered as primary or typical for all Decapoda (Figure 40). The following evidence supports this view, in addition to the obvious usefulness of the structure: 1) clavirostrid types occur especially among the earliest Triassic Decapoda, i. e. the Aulacoceratidae (Zittel-Broili, Figure 1,255) which have to be considered as the predecessors of the true belemnites; 2) many belemnites with a differently formed rostrum have an elongate, clublike "embryonic rostrum" (Stolley, 1911, 1912), which Abel (1916) considered as the distinctive character of a new group, the "Clavirostridae" (Figure 38). This is, however,
112 not an embryonic, but a juvenile structure.

(110)

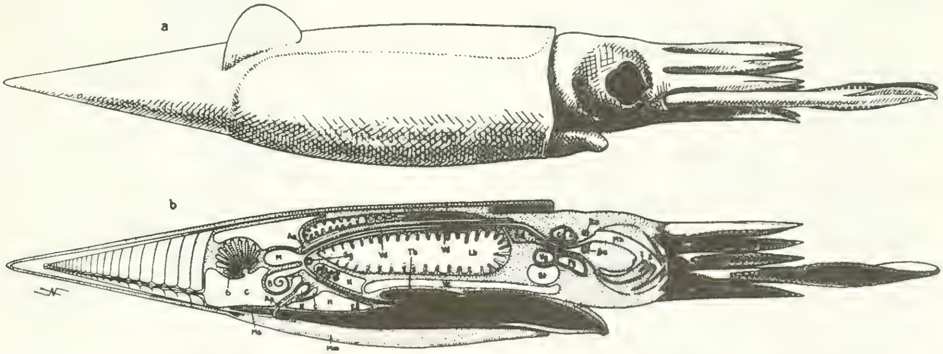

FIGURE 37. Ancestral form of the Decapoda (Protodecapus) in lateral view (a) and sagittal section (b). Compare with Figure 23 (p.91). Note the similarity in the general form, shell form, fin position, the form of the mantle margin and arrangement of cephalic organs. Note the specific form of the tentacle arms, the multiserial arrangement of suckers on all arms and the formation of fin margins on the distal parts on all, except the ventral arms.

However, if we assume a more indifferent, less specialized form of the rostrum for the basic form of all Decapoda (Figure 37), this is done because we must trace back to this basic form a number of other types, including

113 the Sepioidea (q. v.), which require a more massive envelope around the phragmocone. In addition, such an indifferent state of the rostrum is present in a number of fossil Decapoda (Belemnoteuthis, Diploconus) including the most ancient known form (Phragmoteuthis from the Triassic), which in any case has to be considered as the starting point for the Dibranchiata.

(111)

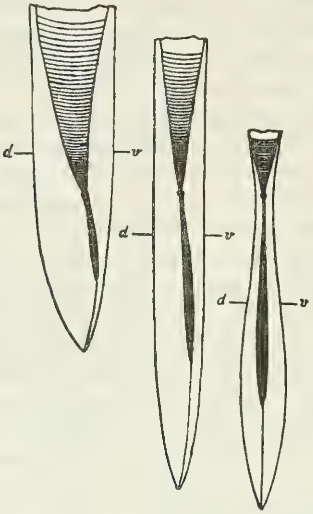

FIGURE 38. Typical rostra of belemnites of the group Clavirostridae (after E. Stolley, 1911, from O. Abel, 1916):

A – Acroteuthis; B – Oxyteuthis; C – Hibolites. The juvenile rostrum (wrongly named "embryonic rostrum") is shown in black. Its bowl-shaped base surrounds the embryonic chamber of the phragmocone. The rostrum remains always club-shaped, whatever its later modification. This juvenile rostrum does not represent the initial part of the rostrum which forms in fact the axial line which is the growth center of the juvenile rostrum (cf. p. 134).

(111)

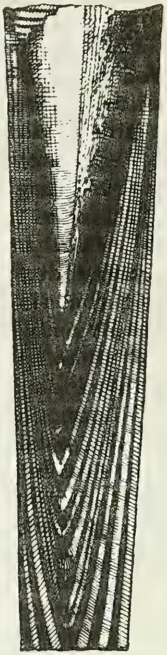

FIGURE 39. Typical example of a "conirostrid" (after F. A. Quenstedt from Abel, 1916). Longitudinal section through the upper part of the rostrum of Belemnites giganteus Schloth (Mucroteuthis Abel). The phragmocone is intact and delimited by the conotheca. The growth layers are actually paper-thin; the figure combines several of them (semi-diagrammatic).

An average form like the conirostrid belemnites (Figure 39) may be considered as the ancestral form of the rostrum of Decapoda. At any rate, both the typical rostrum and its sheath are concentrically stratified and consist of a strongly calcified shell mass.

The proostracum of Protodecapus (Figure 40, p. 112) is distinctly differentiated into middle and lateral plates (Figure 41). The middle plate is pointed triangular. It extends in an acute angle from the rounded anterior end to the end of the cone, its posterior part belonging to the conotheca.

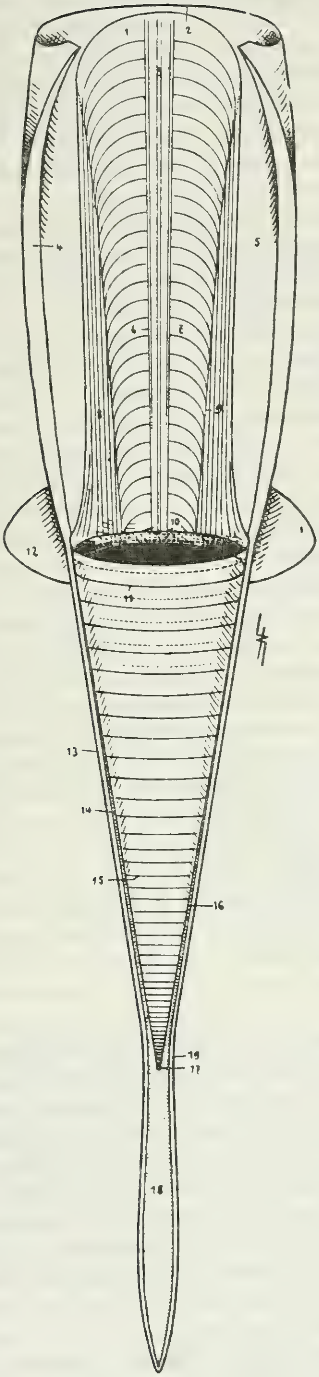

FIGURE 40. Typical shell of Decapoda with club-shaped rostrum in connection with mantle and fins. The figure could be considered as a reconstruction of Belemnites semisulcatus, if this species is identical with Acanthoteuthis speciosa Münster, according to Angermann (1902). The proostracum is drawn after a particularly well preserved specimen of the latter species at the Munich Museum; on the other hand, the rostrum resembles that of B. semisulcatus. The combination appears naturally possible since both have similar proportions. The figure, however, has ideal morphological value and no attempt is made to check Angermann's hypothesis (cf. my book on fossil Cephalopoda).

1 — last formed thin, delicate part of the proostracum; 2 — free dorsal mantle margin; 3 — position of the collar; 4 — section through the mantle (ventral part of the mantle removed); 5 — inner side of the mantle; 6 — median stripe of the proostracum; 7 — lateral part of the middle plate; 8 — lateral plate; 9 — inner line of asymptotes; 10 — ventral margin of the conotheca; 11 — last septum of the shell; 12 — fins; 13 — shell fold; 14 — sheath; 15 — septum; 16 — conotheca; 17 — embryonic chamber; 18 — rostrum; 19 — skin at the transition of the sheath into the rostrum. The fins are inserted slightly too far anteriorly; the phragmocone should be slightly shorter. (Half natural size.)

The lateral plates are more delicate than the middle plate, being thinner and less calcified. They gradually widen posteriorly until their margin passes in an arc into that of the conotheca. As the growth lines show, the middle plate grows relatively rapidly at the anterior margin. The lateral plates are kept in constant proportion with this by the very slow deposition of shell substance at the free margin. The different growth rates are reflected structurally, especially in the formation of fine lines, the "asymptotes," which are formed mainly by the sharp turn of the growth lines but can be thickened by a differentiation of the shell at these points. These "inner asymptotes" are similar to "outer asymptotes" which may be present where the growth lines leave the lateral plates and pass into the conotheca (Figure 24). They may be absent or indistinct if the free margin of the lateral plates is not delimited from the conotheca (Figure 40).

The proostracum can be reinforced on the inner and outer sides by the deposition of new shell layers. The outer layers belong naturally to the secondary shell and pass posteriorly into those of the sheath. These relationships also apply to Protodibranchus, with the limitations made for the rostrum (see above); they were omitted there (p. 92) because they could not be established directly and precisely for the common type. For this, it would be necessary to have comparative data on the Octopoda, which are not available because of the rudimentary condition of the shell in this group. However, the common ancestral form is assumed to have had the common character of the decapod shell, since these alone permit a connection between the typical structures of the Dibranchiata and Tetrabranchiata (Figure 25).

Although this belongs strictly to the domain of internal structure, we shall characterize here the insertion of the fins of Protodecapus for a better understanding of these organs in the following chapters (Figure 41). For Protodibranchus (p. 95) we assumed that the fin base glides against the opposite side of the shell, with the shell and shell epithelium acting as
114 articulation surfaces because this condition is the basis for the complicated relationships observed in the Decapoda. The fins of Decapoda are in fact anchored on the shell epithelium, which is supported at this point by a cartilaginous part of the adjacent mesoderm, the "fin cartilage." This section of the shell sac, however, is already constricted from the remaining part in the embryo by a fold between the fin cartilage and the shell, and the articulation moves on the outer surface of the shell. In Protodecapus, I assume this detachment as still incomplete, corresponding to the embryonic condition (Figure 41).

The formation of such a fold can be explained as a purely mechanical phenomenon i. e. by the displacement of a part of the shell epithelium, which is stiffened by the fin cartilage, on the shell (Figure 26). In recent decapods, the constriction of the articulation pocket at the fin base makes a number of further displacements possible (cf. chapters on Teuthoidea and Sepioidea).

Ontogenetically, the fin musculature develops from the subcutaneous tissue (shell fold) and not from the muscular mantle, as might be assumed from its structure and position in the majority of recent Dibranchiata. The fin is situated primarily on the outer side of the shell, and not on the muscular mantle (see Volume II and Figure 66), although secondary displacements of various types may complicate the picture.

In general, the fins are rounded plates with a thin margin, forming a slight lateral angle and with an incision at the anterior part of the base,

forming a characteristic "earlobe" (Figure 37). The position of their
115 insertion on the outer side of the shell is typical for all Dibranchiata (p. 95).

On the basis of the known fossil, larval and embryonic conditions, however, the fins should be situated slightly further posteriorly than shown in Figures 37 and 40, i. e. on the outer side of the phragmocone behind its free ventral margin, and not extending into the region of the proostracum (cf. Figure 66).

(114)

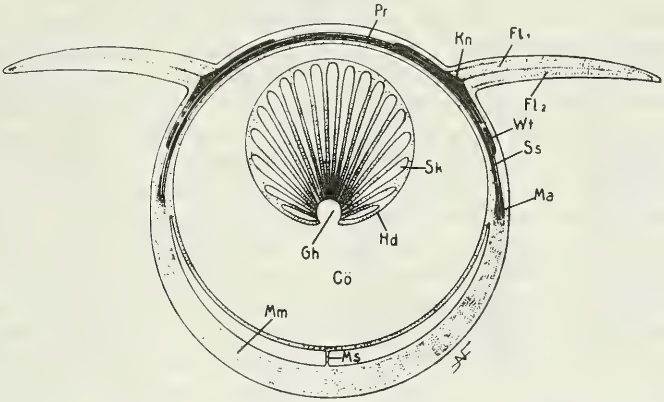

FIGURE 41. Diagrammatic cross section through the posterior part of the body of Protodecapus in the region where the proostracum passes into the conotheca, showing the topographic relationships between proostracum, muscular mantle, mantle cavity, coelom and gonad. The articulation pocket of the fin base is almost detached from the shell sac. The movable fin base is supported by a cartilaginous articulation surface on the fin cartilage. However, the fin base glides on the inner side of the articulation pocket itself, and not directly on the shell (cf. Figure 95):

Pr — proostracum; Kn — fin cartilage; Fl_1, Fl_2 — upper and lower layer of the fin musculature; Wt — articulation pocket; Ss — shell sac; Ma — muscular mantle (origin); Sk — sperm tubules; Hd — testis; Gh — cavity of gonads; Cö — coelom; Mm — muscular mantle; Ms — mantle septum.

The general structure of the head of Protodecapus shows typical conditions in the Dibranchiata. The lid margin and pupil show some minor characteristics.

The lid margin bears anteriorly, between the 3rd and 4th arm, a small indentation where it is tough and hard. At maximal contraction (which persists during the development of many forms) this elastic, membranous-transparent part of the lid covers the eye temporarily or permanently, forming a transparent cornea. The pupil is very variable in outline and also movable; the iris fold moves continually back and forth on the lens, always leaving a transverse opening. The normal condition resembles that in the Loliginidae (see figure), in which the upper margin of the iris extends on the lens like a blinker and is met partly by an expansion of the lower margin. The pupil is usually crescent-shaped, open above; it may also be transverse-oval or nearly circular, in which case the iris flap becomes inconspicuous.

The 10 outer arms are distincly different. The fourth pair,* called tentacles, differs markedly from the others, despite the typical similarities in structure and development, which proves without any doubt (cf. Volume II), that the tentacles are homonomous with the other appendages, which will be referred to further on simply as arms. These "sessile arms" are more primitive, i. e. they are closest to the typical condition of the dibranchiate arm (p. 97). We distinguish dorsal (D), laterodorsal (Dl), lateroventral (Vl) and ventral (V) arms. The arms are connected at the base by little developed membranes, which are absent between the ventral arms, and connect the lateroventral arms directly with the ventral arms, bypassing the tentacles (T-arms) (see below). All arms are quadrangular in cross section, 116 at least proximally. Their inner and outer edges and the two lateral surfaces resemble those of Protodibranchus. As in the latter (p. 97), the edges of the outer side pass into the membranes, while each inner edge bears a row of palplike movable appendages connected by a membranous margin which they support; these structures, very characteristic for Decapoda, will be named protective margin (of the suckers) and protective margin support, respectively. The inner arm surface delimited by the protective margin bears suckers which will be described below (p. 120). The suckers are at first arranged in two alternating rows (cf. p. 98), developing ontogenetically from a uniserial arrangement which develops into a zigzag arrangement which later becomes biserial when the suckers move farther apart to the left and right (cf. Figures 43 and 44a). This process has already been repeated on the tentacles with the exception of the most proximal suckers, so that the arrangement has become quadriserial.**

(115)

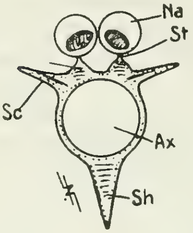

FIGURE 42. Cross section through the distal part of a typical arm of Decapoda. It shows the round muscular arm axis (Ax) surrounded by derivates of primary skin tissue. The outer corners are replaced by a medial swimming margin (Sh) (p.118); the inner corners ar occupied by the protective margin supports (Sc) and the basal pads (not shown) of the suckers (Na), which stand on separate stalks (St). The section is oblique, so that two suckers are cut (cf. Figure 43).

The relationship of the protective supports to the suckers has to be described in greater detail. The primary state is shown in Figure 43. As in Protodibranchus, each sucker is associated with a pair of palps or protective margin supports which occupy the interval on each side between successive suckers. In the Decapoda, however, the palps are always situated closer to the following sucker and appear to belong to it. In almost all forms, the biserial arrangement of the suckers results in the disappearance

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* Counting from above.

** This complication of the arrangement, which may reach a stage of 16 or 32 rows, is easy to understand. In species where the suckers are normally uniserial but numerous, they are arranged in a zigzag pattern which is often very regular in a strongly contracted arm, although the same condition may also exist in a resting arm (in Eledone cirrosa, for example). Individual variations between biserial and quadriserial arrangement are observed especially in Sepia elegans (q. v.).

of the distal palp (Figure 44a) which is hardly ever distinct (compare, however, Abraliopsis). These atrophied palps are marked by small crosses in Figure 43. As a result, each sucker is correlated to a single palp, both being inserted on the same side of the arm. For simplicity, this
117 common condition is shown also for Protodecapus in Figures 110 and 119, although this is slightly inconsistent.

(116)

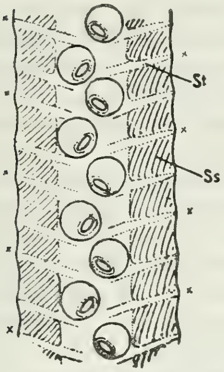

FIGURE 43. Diagrammatic representation of the inner side of a part of the arm of Protodecapus. Note the zigzag pattern of the suckers which are not yet biserial; the typical direction of their openings, the insertion of the "palps" between individual suckers of the zigzag row. One of the palps is inevitably displaced from the coordinated, distally situated sucker and may be lost in some derived forms, leaving only the proximal palp in closer connection with the basal pad of the sucker. In this case, the palp appears to have developed from the sucker support or vice versa, depending on their size (Figure 42):

St — palp or protective margin support; Ss — protective margin.

(118)

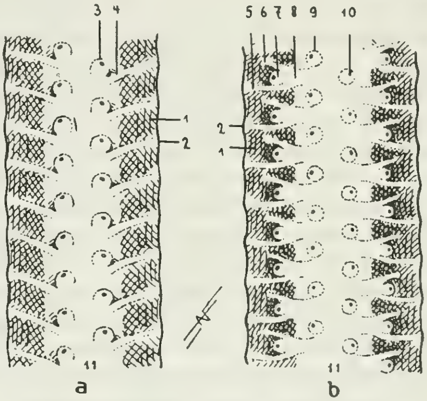

FIGURE 44. Inner side of typical Decapoda arms with bi- and quadriserial arrangement of suckers, after the removal of the latter. The basal pad shows the scar of the removed stalk. Also visible are the light inner surface of the arm and the dark protective margins with the preserved supports connected proximally to the basal pad. Note the loss of one support of each sucker in (a), the connection between the basal pads of the outer suckers and the reduced supports (b) which belong to the median suckers and do not reach the edge of the protective margins, the fusion of the basal pad of the outer sucker with both palps into a pillarlike structure which displaces the base of each marginal sucker to the protective margin:

1 — protective margin; 2 — end of a protective margin support, forming a slight projection of the margin; 3 — basal pad; 4 — base of a support, connected with the basal pad; 5 — support of a marginal sucker; 6 — reduced support of a median sucker; 7 — basal pad of a marginal sucker. 8 — pillar consisting of basal pads and 2 supports; 9 — basal pad of an inner sucker; 10 — scar of stalk of a sucker; 11 — inner surface of the arm.

The process is usually repeated in quadriserially-arranged suckers: those of the median row have no margin supports. However, the corresponding palps persist in some forms (cf. Figure 44 and the chapters on Sepiidae, Loliginidae and Ommatostrephidae).

Our description of the arm apparatus and especially of the suckers and protective margins would have to be greatly modified if we would proceed methodically. Although such an ancestral form would have to be assumed for the known Decapoda and available data on live and fossil forms can be easily traced back to it, there are compelling objections against a direct connection. The type of Decapoda obtained by strict comparison should be even more specialized for the correct interpretation of such otherwise typical Decapoda as the belemnites Gonatus or Spirula. Our form was in fact a Praedecapus, with 2 rows of suckers on the arms and 4 rows on the tentacles. In the true Protodecapus, the originally bilinear and then biserial arm suckers are assumed to have developed from a pattern of 2 zigzag rows which finally changed into 4 rows, while the tentacles bear 8 instead of the original 4 rows of suckers, as can be observed during the ontogeny of Sepia (Volume II).* The form thus obtained will also be named Protodecapus, with the Sepioidea derived directly from it, and the Belemnoidea and Teuthoidea derived indirectly through a transitional form which will be described later (p. 133) as Metadecapus.

Let us now consider the ecological significance of this increase of the sucker rows. The result is naturally an increased number of suckers, sometimes exceeding 100 on a single arm, which clearly improves performance. On the other hand, there is a differentiation and division of work among the different suckers according to their position — a distinct phenomenon in nearly all Decapoda. The median rows are usually more or less different morphologically from the marginal rows (cf. p. 128).

The typical changes of the inner arm surface during the transition into the quadriserial arrangement are shown in Figure 44.

118 The two median rows of suckers remain on the arm axis, removed from the margin. Their palps (6) become reduced without disappearing typically. The "accessory" or protective margin supports are connected with the basal pads of the marginal rows (7), and project together with their own palps beyond the margin, so that the marginal suckers appear to be placed directly on it. In fact, they are situated on a pillar (8) which consists of two palps and the prolonged basal pad, grown together with the seam.

In the multiserial pattern, the marginal rows are generally situated on the protective margin, and this becomes more evident if the number of rows increases. The widening of the tentacle club thus results mainly from the formation of such complicated protective margins, which bear the greater part of the suckers.

On the outer side of the distal part of all except the ventral arms, there is a swimming margin the function of which is to improve the steering action of the arms which are held close together when the animal swims backwards (Figure 32). These structures are absent in the ventral arms which occupy the middle of the outer surface of the terminal part of the arms; the ventral arms have instead longitudinal skin folds with similar action, called here the

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* For a better understanding of this change it is necessary to consider the ontogenetic development of each pattern of suckers (p.107). This explains why the first developed arm and tentacle bases often bear fewer rows than later, since the transition is only secondary. Thus, the base of a quadriserial arm often bears only 2 rows (Sepia orbignyana, Rossia macrosoma, Euprymna morsei, etc.) and this is assumed also for Protodecapus. Similarly, the beginning of the tentacle (stalk part) often has only 2 rows (Figure 50), which become distally 4 and finally 8 rows. The boundary of this transition may gradually move until the quadriserial condition appears only at the end of the arm (Abralia veranyi, Sepiola steenstrupiana; cf. also Heteroteuthis, Sepiola atlantica) or the 8 rows are only evident at the apex of the tentacle (Illex).

lateral margin. This structure is a widening of the outer lateral edges of
the ventral arms extending to the base of the arm, where it is widest and
119 forms the connection to the lateroventral arms. This direct connection is
made possible by the separation of the tentacles from the protective membrane, which is connected with the median and posterior displacement of the base of the membrane, freeing the tentacles from connections which inhibit their movement (p. 120).

The swimming margins are particularly strong on the tentacles. They
probably help steer the animal during the capture of prey. Already at rest,
the tentacles are much longer than the sessile arms, and can suddenly stretch
to at least twice this length by the action of circular and transverse muscles
in the stalk. The prey is first caught by a few terminal, specially differentiated
120 suckers situated on the tentacle apex, which is curved slightly upward and
outward, then the other suckers come into action. Excellent shots, Decapoda capture their prey with a single, rapid movement resembling more a shot than the throw of a lasso (however, see Sepiolidae). Then the grasping arms of both sides begin to work together with great impetus and determination.

Morphologically, the tentacle consists of the following parts: 1) a suckerless stalk, corresponding to a short, inconspicuous proximal part of the other arms; 2) a sucker-bearing club, which can be divided into a stalk part, resembling the stalk but with one zigzag row or two rows of suckers, a widened "hand part" with multiserial, partly enlarged suckers, an adjacent distal part and a terminal part with a few slightly modified suckers (cf. Chapter 5).

Figure 45 shows that the tentacle base is not only detached from the protective membrane,* but is invaginated deeply between the 3rd and 5th arms, the only structure remaining in the plane of the other arms being the ligament which originates in the middle of the inner surface and in the margin of which passes the efferent vein.

The tentacle pocket formed around the invaginated base of the tentacle stalk cannot at first contain the entire tentacle or even a large part of it. The proximal part of the stalk, however, can be retracted into it by contraction (cf. Rossia). In a quietly swimming animal (Protodecapus is assumed to be a strictly nectonic form) the tentacles are extended like the other arms, with the ends of the arms close together as was assumed for Orthoceras and Protodibranchus (Figure 32).

The suckers of Decapoda (Figure 29) are highly differentiated, particularly with respect to the mechanization of their function. The components of a sucker are mainly the same as in Protodibranchus and the Octopoda, namely a marginal ring, adhesion ring and suction chamber with chamber floor, chamber ring and chamber margin, and a support. The chamber floor, however, is thickened into a suction pad and connected with the support (or basal pad) by a thin stalk. Opposite the stalk, the chamber floor is deepened into an eccentric, funnel-like depression, while it forms a characteristically loose (membranous) connection with the chamber wall at the margin. As a result, a pull at the stalk (by prey trying to escape) actually increases the adhering capacity of the sucker by retraction of the suction pad (Figure 46). The chamber wall takes part only passively in this suction; it no longer supports the suction chamber by muscular action, but strictly mechanically

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* Compare the behavior of the hectocotylus in the Argonautidae.

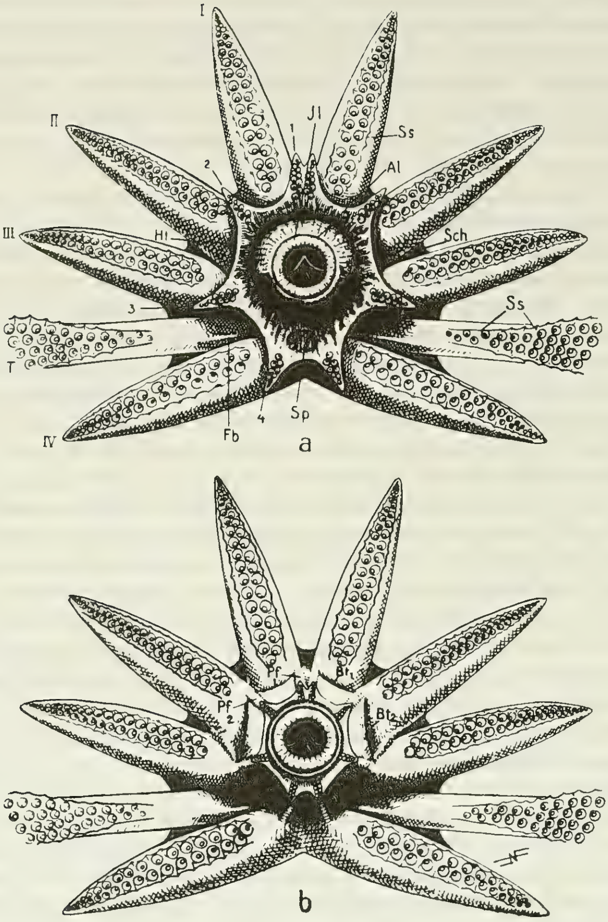

FIGURE 45. Mouth area of a female Protodecapus with spread arms: a) with open and b) closed buccal funnel. Note the general arrangement of the grasping arms (I–IV), buccal pillars (oral arms, 1 – 4) and the arrangement of the suckers. Particularly important details are the buccal membrane (Ht) between the oral arms, the protective membrane (Sch) between the outer arms, the ligament (Fb) on the tentacle base, the 3 pocketlike depressions (bucal pockets, Bt 1 – 3) on each side between the outer and oral arm series, the depression (Sp) between the ventral oral arms on the inner side of the protective membrane for the reception of spermatophores (in the female!), the projection formed by the mouth (oral cone) with the outer lip (Al), inner lip (Il) and jaws (H). Ss – protective margins.

with its solid cuticular layer (horny ring). The adhesion ring is also cuticular and it bears a characteristic, regular pattern of rugosities, papillae or denticles which prevent slipping. Much stronger teeth of similar type (Plate XIII, Figure 6) are situated at the boundary between adhesion ring

121 and horny ring, i. e. at the margin of the latter. These teeth are pressed into the skin of the prey when the grasping ring of the sucker adheres closely, and markedly strengthens the action of the sucker, especially when the prey has a soft yielding skin (cf. p. 127). Such a sucker functions as a clawed paw and often looks like one (Plate XIII, Figure 7). Being smooth and soft, the marginal ring effects initial adhesion of the sucker, while pulling increases the effect strictly mechanically. A special mechanism for detachment is obviously necessary: a group of muscular elements on the outer side of the sucker at the highest part of the chamber wall detach the marginal and grasping rings and permit water to enter through the margin into the suction chamber. I also observed (e.g. in Loligo vulgaris) that with strong pulling of the attached sucker a small gas bubble enters the suction chamber, apparently from the depression on the chamber floor (suction pad) opposite the stalk. The muscle ring around the posterior part of the chamber wall (Plate XIII, Figure 7) may participate in detachment, but it cannot be of essential importance since it is absent in all the Oegopsida observed (Ctenopteryx?); the ring is not completely closed also in Loligo, but it is fully developed only in the Sepioidea (q. v.). In contrast to the Octopoda and Protodibranchus, the suckers of Protodecapus are no longer strictly radial symmetrical, but are bilateral. The distal (with respect to the mouth) wall of the chamber is higher than the proximal wall, and the distal margin is more strongly dentate; the stalk is also
122 inserted eccentrically near the proximal edge of the chamber floor like the depression opposite the stalk. Contraction of the small median muscle on the outer side of the distal wall of the chamber which detaches the grasping and marginal rings causes a deformation (Plates XII and XIII), which is nearly always visible on preserved suckers.

(121)

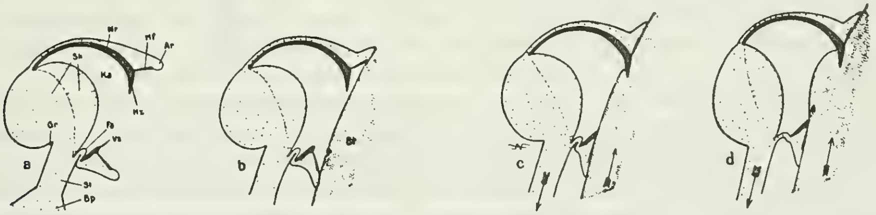

FIGURE 46. Suckers of Illex coindeti in different stages of function. Diagrammatic median sections, highly magnified:

a — resting position; b — first adhesion to a smooth surface; c, d — effect of escape attempts of prey and countermove of the predator (arrows); Gr — pocket into which the stalk is inserted; Sk — suction pad; Ka — suction chamber; Hr — horny ring; Hf — adhesion ring; Ar — marginal ring; Hz — main tooth; Fa — fold, actually the narrowest place of the suction pad area situated below the eccentric pocket; Vz — smaller tooth; St — stalk; Bp — basal pad; Bt — prey. The conditions resemble in principle those shown in Figure 29c, but differ in the markedly eccentric insertion of the stalk and the lack of circular muscles in the Teuthoidea or Oegopsida. The function illustrated here is stictly mechanical and persists as long as 24 hours after death, when decomposition has already begun. Detachment of the suckers takes place by gliding if there is no pull.

The mouth area is of particular interest. As in Protodibranchus and the Tetrabranchiata, there is a circle of oral arms, known as the buccal funnel in Decapoda, inside the outer arms. This inner circle consists of 8 small, rudimentary arms (buccal pillars) the inner side of which bears 2 rows of suckers as at first on the outer arms (p. 116). The oral arms are connected by a relatively large membrane with a warty, rugose inner surface (p. 119). The mouth cone which is situated inside the buccal funnel is surrounded by a deep circular groove and can be retracted or considerably projected. The rudimentary oral arms or buccal pillars project in edges on the outer side of the buccal funnel (Figure 45b) and each oral arm is associated with the base of one outer arm: the upper 4 buccal pillars are attached on the median inner edges of the upper 4 outer arms, the 3rd pair more on the ventral side of the 3rd arm, and the 4th pair medially on the ventral pair of outer arms. These attachments have no direct connection with the proximal ends of the membrane of any arm.

The dorsal buccal pillars are situated close together and become fused at an early stage in most Decapoda (see Volume II). The resulting structure is related to both dorsal arms, but behaves as a single arm with only one ganglion and 2 rows of suckers like the other buccal pillars. A similar condition may perhaps be assumed already for Protodecapus (see, however, Chapters 9 and 12).

The mouth shows no special characters. The margin of the inner lip surrounds the cut-off surface of the truncate mouth cone (see p. 119), which usually projects more in Decapoda than in Octopoda.

The jaws of Decapoda differ from those of Octopoda in the better developed biting processes, which are more or less distinctly delimited (Plate XVII). The radula of Decapoda shows no typical characteristics, and resembles that described for Protodibranchus (Figure 32; Plate XIV, Figure 1).

A significant new development is the funnel system of Protodecapus. In Tetrabranchiata and Protodibranchus the only firm connection between the funnel and mantle is dorsal, by the collar. In the Decapoda, there is also a ventral connection by the funnel cartilage which develops usually only in the postembryonic stages (Figure 47). Like the neck cartilage (as the collar is called), the funnel cartilages are hard surfaces with a marginal edge, cartilaginous at least in the posterior part, adhering to the inner side of the mantle and gliding there without losing adhesion. In Protodecapus, they have the form of narrow, longitudinal ovals with a shallow groove-shaped depression. Opposite them, the inner side of the mantle bears thin longitudinal ridges, the mantle cartilages, the tissue of
123 which is also firmer than the rest of the mantle, without being uniformly cartilaginous. Like the gliding surface opposite the neck ("collar bond"), these ridges are longer than the adhesion apparatus opposite them and extend anteriorly to free mantle margin. This structure attaches the funnel apparatus to the mantle opening, improving the efficiency of the funnel. This new development is therefore not merely a complication of form but a progress in adaptation in a direction described above (p. 100).

As to terminology, I suggest that the terms funnel cartilage, mantle cartilage and nuchal cartilage be replaced by "funnel bond," "mantle bond," "neck bond" and "collar bond" because the development of cartilage is not general and is not an essential character. These terms will be used in the following descriptions.

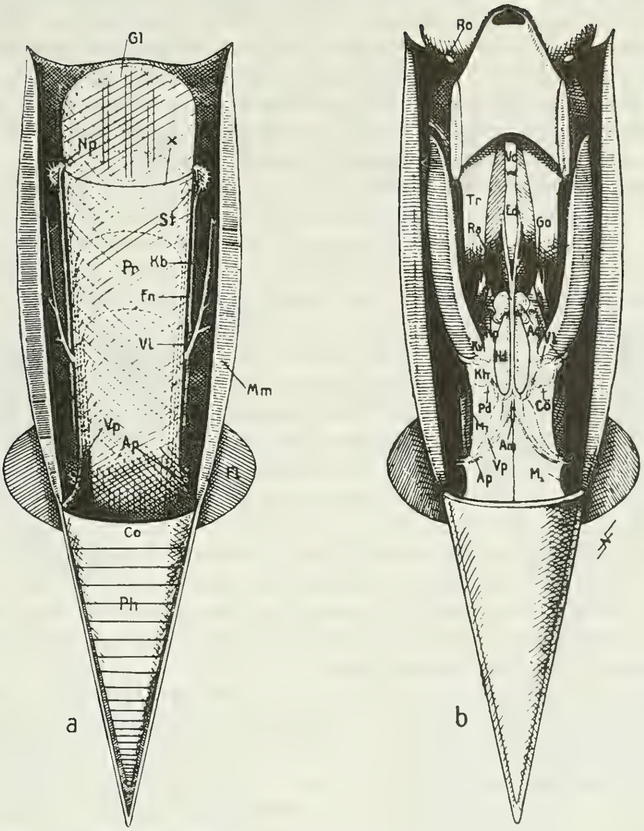

FIGURE 47. Shell and situs of mantle cavity of Protodecapus:

a) Shell situs. The mantle situs is emptied so that only the lateral parts of the mantle with their attachments and the shell remain. All essential characters resemble those of Protodibranchus as shown in Figure 34, because the primary shell of Octopoda is unknown, and the condition of Protodibranchus is constructed mostly from the available data on Decapoda, but with closer similarity to the Tetrabranchiata. Gl — collar bond, i.e. adhesion and gliding surface for the neck bond; Np — pallial nerve, posterior border of the dorsal mantle cavity; St — stellate ganglion; Kb — branchial attachment on the mantle; Pr — proostracum; Fn — nerve of fin; Vl — lateral pallial vein, passing on the inner side of the mantle; Mm — section through the muscular mantle; Vp — posterior pallial vein, entering the mantle; Ap — posterior pallial artery; Fl — fins; Co — conotheca; Ph — phragmocone.

b) Mantle situs after removal of the ventral part of the muscular mantle. Note the funnel bonds, translucent ink sac, renal papillae (Np) which are displaced anteriorly, form and attachment of the gills; the entry of the pallial vessels into the mantle (Vl, Vp, Ap), the formation of the median pallial septum and the genitalia. Since an immature female is represented, it has accessory nidamental glands (Ac) between the renal papillae, as well as true nidamental glands (Nd) situated above the renal sacs, and large genital processes (Go) on each side of the gill root pockets which open forward and outward. Ro — olfactory organ; Vc — vena cava; Tr — infundibular retractor; Ed — intestine; Ra — musculus rectus abdominis; Go — genital process; Ac — accessory nidamental glands; Vp — renal pore; Kv — branchial vein; Nd — nidamental gland; Vl — lateral pallial vein; Kh — branchial heart; Pd — pericardial gland; Cō — branchial heart pocket of coelom; M_1, M_2 — remnants of the primary mantle; Am — median pallial artery; Vp — posterior pallial vein; Ap — posterior pallial artery.

Despite the presence of the "closing apparatus" between mantle and funnel, the funnel apparatus can still glide in the longitudinal direction within the mantle opening, so that it permits vigorous swimming movements (see p. 100) without losing the solid connection between the parts as they move against one another. The possibility of gliding is particularly important for the action of the powerful cephalopodial and funnel retractors, which reduce the volume of the mantle cavity rhythmically.

The organs of the mantle cavity of Protodecapus resemble those of Protodibranchus in all essential aspects (p. 101), but there are some differences. The gills are very long and thick because of the increased muscular activity. The ink sac is enlarged and visible through the skin, but only its outline is visible, not the color of the ink, since the sac is covered by a glistening membrane (argentea). The genital processes project distinctly and are covered by the gill roots only in young specimens; they are later gradually displaced toward the anus (Figure 47b).

In specimens with moderately filled intestine, the proostracum projects laterally above the abdominal complex, as was also indicated for Protodibranchus (Figure 35). The proostracum is here still covered by the primary mantle (p. 94), while the muscular mantle is attached only at the margin (cf. Loligo vulgaris).

The female organs in the mantle cavity resemble those of Protodibranchus (p. 105). The female genital process, i. e. the projecting part of the genital duct, is markedly thickened at the base and contains the oviduct gland, which resembles the nidamental gland in structure and participates in the formation of the egg membrane.

As in Protodibranchus (Figures 33 and 35), the nidamental glands develop at a typical point where a small area of ectoderm is invaginated into a sac with a round opening (cf. Nautilus, p. 74). In each sac later develop the gland lamellae and the sac expands anteriorly and posteriorly until it occupies an area like that of a renal sac in the abdominal complex (Figure 47b; cf. 125 Loligo vulgaris). The fully developed nidamental glands are massive whitish formations, the lamellar structure of which is visible through the skin (Plate VII, Figure 49). The slits between the booklike lamellae open into an also translucent longitudinal slit which carries the secretion to the anteriorly situated opening.

The two accessory nidamental glands (cf. Döring, 1908) are situated anterior to the nidamental glands, typically in the median area between the renal papillae. They develop after the nidamental glands and consist at first of two round spots of thickened epithelium on which later a system of radial ridges and grooves develops (Figure 48). A regular series of deeper depressions — "anlagen" of the gland tubules — develops in each groove from the center. The central tubules always develop before the peripheral ones, but all of them deepen markedly and finally have the same structure, so that the gland becomes massive and padlike (Plate II, Figure 2) and its entire surface is densely covered with radial rows of glandular pores. Later, the skin surrounding the pad closes above it (cf. chapter on Sepia) and gradually reduces the opening of the gland, while normal skin covers the marginal parts of the gland. The temporarily enormous glands decrease gradually in size, while the at first minute nidamental glands grow and become rapidly larger than the accessory glands. Finally, the nidamental 126 glands partly overgrow the constricted opening of the accessory glands, and apparently prepare a combined secretion of the two glands. The function of these is obscure, especially that of the accessory glands. The viscous, sticky secretion of the nidamental glands is apparently difficult to use, while the mucus of the accessory glands may facilitate the formation of the egg membrane as a mechanochemical agent. (But compare also the luminescence of these organs in the chapter on Sepiolidae.) At any rate, the action of the accessory glands is apparently not indispensable, as the Oegopsida lack such glands (floating egg masses), and accessory glands are present only in the Loliginidae and Sepioidea, which attach the eggs.

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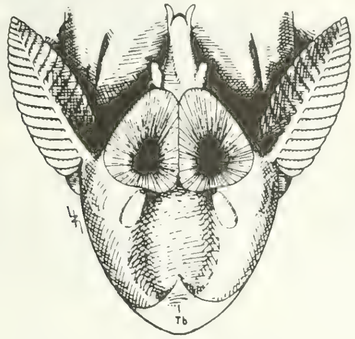

FIGURE 48. Mantle situs of a young Sepia elegans (6×). The following parts are shown: the anal papilla; behind it laterally the two renal papillae; further posteriorly the "anlagen" of the accessory nidamental glands with their radial structure in the center of which are the "anlagen" of the glandular tubules; further posteriorly are the small nidamental glands on either side of the ink sac (Tb) which extends far posteriorly; around the ink sac passes the median pallial artery, which has been cut at the entry into the mantle. To the right and left of this point is the posterior boundary of the mantle cavity, which does not quite reach the posterior end of the body. Also visible are the posterior parts of the funnel retractors, the gills and, behind them, the translucent branchial hearts.

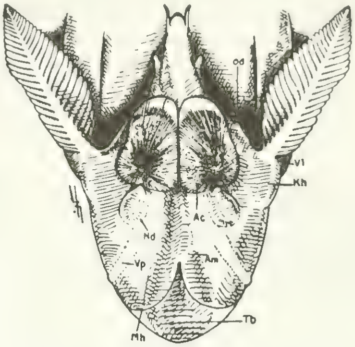

FIGURE 49. Similar figure of a young Sepia orbignyana (2×). The illustration shows the further development of the nidamental glands (Nd) and of the accessory nidamental gland (Ac), especially the formation of glandular tubules (dark zone) in the marginal and anterior parts:

Od — juvenile genital process; Vl — lateral pallial vein; Kh — branchial heart; Am — median pallial artery; Vp — posterior pallial vein; Tb — ink sac; Mh — posterior border of the mantle cavity.

Protodecapus is assumed to show sexual dimorphism also in the general proportions of the body with relative enlargement of the head and strengthening of the arm apparatus in the male, and enlargement of the posterior part of the body and of the shell in the female (see chapter on Illex). Sexual dimorphism was probably also manifested in the tentacles, as many female Decapoda (Sepiolidae, Loliginidae, Ommatostrephidae, etc.) collect material for the large egg masses with their much better developed tentacles.

Hectocotylization (p. 86) in Protodecapus consists of an enlargement of the suckers in the proximal and middle parts of all arms, as in Protodibranchus, and in a less marked specialization of the normal part of the left ventral arm for the transfer of the spermatophores. The copulatory arm may be only slightly modified, since hectocotylization later proceeds in various directions among Decapoda, also if this arm acts as a true hectocotylus. It is impossible to determine a general type, although this is probably a reminiscence of the ancestral form of Decapoda, since the left ventral arm serves as copulatory arm in so many forms.

During copulation the spermatophores are attached at the typical point, i. e. on a specially prepared area below the mouth, ventrally on the inner side of the buccal skin (Figure 45).*

c. TYPICAL POSTEMBRYONIC DEVELOPMENT

In general, the typical postembryonic development of the Decapoda follows the pattern described for the Dibranchiata (p. 107, Figure 36). The specific characters of Decapoda, however, appear already in the free young stages (Figure 25d), although they are less marked than later. The tentacles differ only slightly from the other arms in the young stages of most Decapoda (except in species with particularly large eggs, which hatch late). The suckers of young decapods are still undifferentiated (Figure 29); they are
127 at first uniserial, but begin soon to form a zigzag pattern (Volume II, Plate XXI). In this manner develops a biserial arrangement, which soon becomes quadriserial when each of the two rows spreads into a zigzag pattern. The biserial arrangement persists at the base of the arms in the type. At the tentacle base, this is followed gradually by a quadriserial and octoserial arrangement (see p. 117). The buccal funnel is represented at first only by the papilliform "anlagen" of the oral arms (buccal pillars), which later grow and develop suckers and the membrane which connects them. The funnel bonds and mantle bonds are still absent, and the genital organs are still in an early stage of development in the mantle cavity (cf. Volume II). Sexual differences in the arms and body proportions become evident only in the mature animal.

The shell and fins of young forms show a number of specific characters. The shell naturally lacks at first a periostracum; when this appears, a true rostrum is still absent (cf. Sepia and Spirulirostra). The rostrum becomes distinct only after a number of chambers has been formed.

The fins are relatively small and little developed, especially after the elongation of the body; there is no "earlobe" and lateral corner (in all decapods; cf. the youngest stages of Oegopsida). The fins are simple, rounded lobes, which are widest at the base (cf. Volume II, Plate VIII; Figure 66).

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* In some groups, however, the spermatophores are placed directly in the mantle cavity, or the behavior varies (e.g. in Loligo; q.v.).

d. VARIATION OF THE TYPE OF DECAPODA

Metamorphosis proceeds in three directions corresponding to the suborders Belemnoidea,* Teuthoidea and Sepioidea (pp. 46—49). The last suborder is quite independent (cf. Chapter 37), while the first two show closer relations which suggest a common ancestral form which we shall call "Metadecapus" in which the suckers and organs are arranged in a complicated manner. During the postembryonic development, some of them develop into hooks like in the Belemnoidea and Teuthoidea. Already in Protodecapus (p. 121) we assumed that the teeth at the distal edge of the horny ring function like claws in grasping prey, particularly the median tooth which is the most prominent in size and position in many cases (Plate XII). Some cups may become further differentiated as suckers, others may develop into claws. The latter condition is more appropriate for the cups, which hold the captured prey, i. e. the larger and more proximal suckers, which are less able than the small terminal suckers to take hold of the prey rapidly (e.g. smooth, hard-shelled Crustacea). The two types of weapon may also be used against different types of prey (soft- and hard-shelled). The recent species Gonatus fabricii (q. v.) illustrates the significance of the conversion of the suckers into hooks for division of labor. On the basis of this example, I assume that the conversion of suckers into hooks in the postembryonic stages of Metadecapus is restricted to the 2 inner rows of the arms and the 4 inner rows of the tentacles (which may also be 2 zigzag rows), while the simple marginal rows of the arms, the zigzag-shaped marginal rows of the tentacles and the proximal and distal parts of all grasping arms retain the primitive dentition of the original suckers. The varied conditions in fossil and recent Decapoda can be best understood on the basis of such arrangements.

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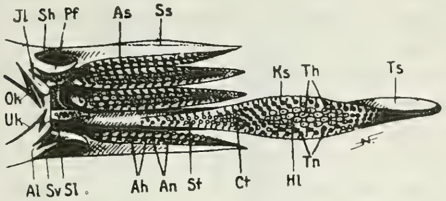

FIGURE 50. Arrangement of suckers and hooked suckers in a young stage of Metadecapus. The arms bear 4 rows of suckers, the tentacles bear 4 zigzag or 8 simple rows. Suckers that are in the process to be transformed into hooks are on the 2 inner rows of the middle part of the arms and on the 4 inner rows on the tentacle club:

Jl — inner lip; Sh — connection of membrane; Pf — dorsal buccal pillar (oral arm); As — protective margin; Ss — dorsal swimming margin; Ks — protective margin of tentacle club; Th — hooked suckers of tentacle; Ts — swimming margin of tentacle; Tn — tentacle suckers; Hl — inner surface
128 of the tentacle (hand part); Ct — carpal part; St — stalk part; An — arm suckers (marginal row); Ah — hooked suckers of arm (middle row); Sl — membrane of buccal funnel; Sv — same, medioventrally; Al — outer lip. The illustration can be directly combined with the main diagram in Figure 37, giving a complete picture of Metadecapus.

For a better understanding of the assumed displacement, it is necessary to bear in mind that the inner and outer rows become differentiated also in the Sepioidea with a typical (quadriserial) pattern of suckers on the arms, as in all decapods with quadriserial tentacle clubs in which this differentiation proceeds in the same direction, but in a lesser degree (cf. Sepia officinalis). This phenomenon, which is so marked in Gonatus and typical for the "Metadecapoda" can, therefore, be traced back to a more general condition, possibly that represented by Protodecapus (p. 120). However, since this is too little market, it will not be further discussed.

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* Diagnosis: Belemnoidea are Decapoda with a well preserved, straight phragmocone and with hooks on the arms or on part of them. Our type of Decapoda and the hypothetical ancestors of recent Decapoda should naturally be placed near the Belemnoidea. If such forms really existed, it would be necessary to omit the 2nd part of the diagnosis, and the suborder would appear then as the central group of the whole order (p.16).

The Gonatus-like formation of cups and hooks cannot be accepted as the primary pattern in the group. Since the majority of the relatively large number of recent Decapoda with hooks on the arms have 2 rows of attachment organs on the arms and 4 rows on the tentacles, the ancestral form may have been similarly equipped and the condition may have been retained in the descendants. This is all the more plausible since the biserial condition of the arms (p. 116) has to be assumed in any case for an earlier
129 stage. On the other hand, an otherwise primary genus such as Gonatus, or the numerous hookless forms, could then not be derived naturally from such an ancestral form. There is no possible path from this condition to all of these forms without hooks. If arms were equipped with only 2 rows of highly differentiated, not cuplike hooks on most of their length, as probably was the case in the fossil Belemnoidea and Teuthoidea, a return to typical suckers would be excluded. Furthermore, also the cuplike ontogenetic stages (cf. p. 131) are not fully developed, typical cups, and consequently could not appear again as inhibited structures. At any rate, such an assumption would require a multitude of other hypotheses, convergence, parallel development, etc., and would contradict our main principle (p. 10). Typical suckers can develop into hooks by a metamorphosis (i. e. phylogenetically); the opposite is impossible since it would involve ecological regressions, which is contrary to nature (p. 10) in view of the special process of modification (p. 130).*

These premises permit to arrive simply and naturally at all the specific differentiations and patterns of suckers and hooks among the Metadecapoda. It is particularly easy to explain the forms in which either suckers or hooks alone are arranged in 2 rows on the arms and in 4 rows on the tentacles. Functional suckers and hooks were both assumed to have existed in the original form. One became dominant at the expense of the other (p. 127), resulting in a simpler arrangement, which has to be interpreted as an inhibition of the typical development (p. 117). Suckers of the marginal rows entered the middle rows or vice versa, so that an ever larger part of the arm base remained biserial (Figure 50). The loss of the special position resulted in the loss of the special character because of ecological and developmental-dynamic factors (but see p. 132). The question is not necessarily ecological, why a reverse differentiation could occur after it appeared as an adaptation (p. 127). It should be remembered that such "progress" is related to a certain type of prey and may become unimportant after a change of diet. In my view, the loss of hooks is a one-sided specialization to a crustacean diet, while the development of hooks is an adaptation for the capture of soft-skinned animals as fish and molluscs, especially Cephalopoda.*

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* I do not refer to the statement that organic processes are irreversible and that their duration is clearly determined, in spite of all theories of relativity. Neither shall I consider Dollo's law, which I reject altogether. A return to phylogenetically earlier conditions is quite conceivable and can be proven if such proof is at all possible (cf. concluding section 2). My concept is based on specific objective considerations as well as on generally determined methodical principles.

130 The evaluation of these general considerations requires a more exact knowledge of the development of hooks.

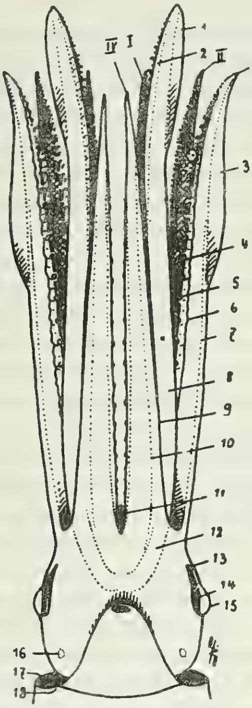

FIGURE 51. Head and arm apparatus of Metadecapus. Ventral view:

I–IV – arms of the left side; 1 – swimming margin of tentacle club; 2 – ventral protective margin of tentacle club; [3 – 7, parts of third arm] 3 – swimming margin; 4 – hooks (medioventral row); 5 – sucker (lateroventral row); 6 – ventral protective margin; 7 – ventral outer margin; 8 – tentacle stalk; 9 – lateral edge of ventral arm; 10 – line of origin of ventral arm; 11 – mouth; 12 – invaginated base of the tentacle stalk; 13 – eyelid sinus; 14 – eye bulb; 15 – lens; 16 – olfactory papilla; 17 – funnel pocket; 18 – ventral corner of the mantle margin.

(131)

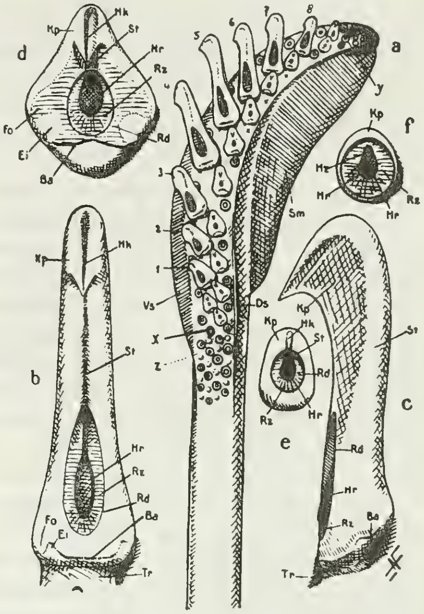

FIGURE 52. Right tentacle club of a young Ancistroteuthis (q. v.). Note the structure of the large and small hooks of the central figure (a), which are shown separately in (b), (c), and (d). x x x are lost suckers; (e) – cuplike, rudimentary hook; (f) – hooklike suckers, designated as x in the central figure:

kp – hood; Hk – hooks; St – stalk of hook; Hr – horny ring of the original cup; Rz – attachment ring of the original cup; Rd – marginal ring; Ba – basal part of the modified horny ring; Ei – typical depression; Fo – process of the latter; Tr – sucker- or hook-support; y – distal hooklike sucker, like (f); Sm – swimming margin; Ds – dorsal protective margin; Vs – ventral protective margin; z – carpal buttons.

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* See ecological part. My view is based on examination of the intestinal content of various types, i.e. on special objective considerations as well as the generally established methodical principles.

Plate XII shows that even true suckers may be clawlike. This also applies to such forms as Loligo and Illex, in which true hooks are absent (or no longer present?) which has to be expected on ecological grounds. In forms with true claws (hooks), the adjacent normal suckers would certainly not be expected to assume clawlike functions as much as in forms in which only suckers are present.

Already true suckers bear a prominent tooth ("main tooth") on the horny ring in the middle of the distal margin. A more accentuated condition of this tooth leads easily to the form shown in Plate XII, Figure 9, i. e. a structure intermediate between a sucker and a hook. Such a structure could still function as a sucker; the marginal ring is raised more strongly near the hook as if to move over it. Thus, an initial hold is automatically strengthened by pulling (Figure 46) when the tooth is pressed against the prey and penetrates it after a short glide in the direction of the pull (in the case of soft-skinned prey).

Such intermediate stages between sucker and hook undoubtedly made the transition possible in the phylogenesis of Metadecapus in which they probably occurred together with hooks and suckers. I have examined recent species for the presence of such patterns and believe that this condition is also present in Gonatus (although I had only a small and badly preserved
131 specimen). In the other recent genera, such structures are present only in a single logitudinal row in the transitional zones between suckers and hooks and are always rudimentary (inhibited development). A predetermined and complete specialization probably takes place. The indicated points bear structures which agree with our scheme (Figure 52) as far as they are distinct. Thus, I found numerous such structures in a young Ancistroteuthis. Figure 52e shows a kind of primitive hook. It appears as if the middle tooth of a sucker has become longer and curved, and that parts of the horny ring are included in the stalk of the newly formed hook, which is typical for such organs. Further, the marginal ring has been constricted like a protective skin which forms a sac above the hook and attachment ring, which is also typical for true hooks. The end of the hook projects from the narrow opening of the marginal ring, the hook sac (cf. Pyroteuthis); in other cases the sac is closed completely and has to be pierced during function, if it is not retracted rapidly (Figure 52 b, c). The former behavior is usually present in the shorter hooks of the arms, while the latter is characteristic for the large, long hooks of the tentacle club.

The suction chamber disappears during the transition to a hook. The horny ring which supported the suction chamber now assumes the task of anchoring the hook in the body of the cup. A remnant of the suction chamber usually persists, and even the opening is often still visible. The attachment of the hooks on the arms also becomes changed. The hook supports are always very low but usually distinct, while the stalks are stronger than in normal suckers. The tentacle clubs bear large and small hooks although there are transitions. The large hooks have a broad base on very strong, short
132 supports and no clearly defined stalk, and the hooks have a long stalk (Figure 52e). The small or "rotatory" hooks have short, thin stalks. Their rounded posterior surface is situated in an articulation pocket, permitting rotation. The small hooks are variously arranged, often opposed to each other. The large hooks, on the other hand, are always direct anteriorly and

laterally. The normal outer arms usually bear more undifferentiated, intermediate types of hooks.*

If hooks are replaced again by suckers during metamorphosis, this should not be interpreted as a retrogressive transformation. Suckers can develop into hooks (Plate XII), but not vice versa. Hooks are highly specialized organs, of which the gradual conversion into suckers would cause a loss of efficiency, which cannot be assumed according to our basic principles (p. 10). All transformations assumed here must be naturally possible, viable and useful. Thus, if typical hooks had only a small suction effect, which would be of no use to the animal, they would be defective as hooks. Hooks are differentiated far beyond the "neutral state" (Plate XII, Figure 9) in which both functions are balanced. The same may be said of the possibility of the conversion of the swim bladder of a physoclist into a lung (cf. p. 129). Replacement of hooks by typical suckers, however, is possible. Suckers can individually take the place of hooks in a large variety of forms with hooks (Onychoteuthoidae, Enoploteuthidae, etc.); the number of the undifferentiated "anlagen" is not fixed in any species. The morphogenetic potencies which determine transformation may sometimes affect adjacent structures, or vice versa. As a result, the boundary between the hook zone and the normal sucker zone (p. 128) may shift in either direction, although not the whole transitional series appears if the change is at the expense of the hooks. The conversion of suckers into hooks usually does not affect the whole of the longitudinal rows on the arms; normal suckers remain in the areas proximal and distal to the hooks. This condition is assumed to be the case also in Metadecapus. Compare the Oegopsida and their development on this point.

133 The type Metadecapus, a metamorphosis of Protodecapus, determines the origin and morphology of the Belemnoidea and Teuthoidea, and permits to understand them in many problematical points, especially the relationship between the fossil and recent species. It is striking that all fossil forms studied have hooks** and not suckers, although the hooks are modified suckers. Conversely, hooks are replaced by suckers in most recent species. This can be explained by the above considerations, although one would expect the opposite. There is also another problem: Belemnites, generally regarded as close relatives of the predecessors of all Decapoda, are believed to have had only 6 arms (cf. Abel, 1916), a condition which appears to recur in young Oegopsida (q. v.). This would mean that the number of arms in the Decapoda would have increased secondarily, which

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* It must be pointed out that the hooks of the fossil forms differ both among themselves and from those of recent species. Particularly, the attachment of the hook base to the rudiment of the true sucker was probably very different. I am best acquainted with two types, the type common among belemnites ("Acanthoteuthis conocauda"), which is common in Liassic slates, and "Acanthoteuthis speciosa" from lithographic slates of the Upper Jurassic. Aberrant forms of claws occur also among recent Teuthoidea, which will be described in part in the special section and in the book referred to on p.58.

Many of the hooks named "onychites" in collections certainly do not belong to Cephalopoda. These hooks, some of which are very large, have a quite different form (cf. Zittel-Broili), but they cannot have been inserted and used in a manner known for Cephalopoda.

** This fact proves their true character as Decapoda, since a sucker of Octopoda could never develop into hooks (Figure 29). The number of arms is unimportant in this respect. There are also Depacoda with 8 arms (Octopodoteuthis, Leachia, etc.). Naturally, the shell of the fossil forms shows also other systematic characters of the order of Decapoda (p.110). (Cf. later my "Fossil Cephalopoda").

is very improbable.* In my view, the fact that no more than 6 double rows of hooks are found instead of the arms of belemnites indicates merely that suckers were probably still present on the other 4 arms, and not that only 6 arms were present as Abel believes (cf. also Crick, 1910; Stromer, 1912). It is much more important to prove (see below) that belemnites were typical Decapoda in their systematic character (irrespective of a conceivable reduction of the number of arms) than to determine the number of arms from badly preserved fossils. This would provide definite information on their structure: the typical morphology of Metadecapoda is assumed until the opposite is demonstrated. The reconstructions of Abel ignore all systematic-morphological principles. For further criticism of his approach, my own attempts referred to (p. 58). My concepts are illustrated in Figures 50 and 51. Insofar as formation of hooks on the arms is concerned, many belemnites probably resembled Gonatus fabricii (q.v.), i.e., that their ventral arms usually bore only suckers. The tentacles are unknown On the whole, very little is known of the Belemnoidea in general, and on the belemnites in particular. Despite the large amount of material, abundant literature and the large number of more or less fanciful reconstructions, no single complete belemnite shell is available for a methodical reconstruction of the animal. (For this purpose, the free margin of the conotheca and that of the proostracum must be preserved.) Even the impressions and petrifications of parts of the head and arms are insufficient, and all the evidence
134 available can only provide suggestions for a systematic construction of the typical on a systematic and morphological basis, as attempted here. This approach also provides the principles for the interpretation of individual fossils.

I would like to stress another point. The mass occurrence of rostra of belemnites has stimulated a special interest in these parts. The knowledge obtained was applied prematurely for the interpretation of the shells of recent and fossil relatives. A detailed description of a belemnite rostrum cannot be given here, but some brief remarks are necessary. The septal ends of typical belemnites are highly differentiated in growth and structure. They cannot be directly related to those of the recent Teuthoidea or Sepioidea, or to those of the Spirulirostra, Beloptera and related Sepia-like forms. These structures consist of two elements which differ in the type of growth (i. e. the transversely stratified "axial part" formed by terminal growth of the needle-thin juvenile rostrum; there is no "embryonic rostrum"), and the stratified, radially fibrous cortical part which surrounds the former and merges concentrically without boundary with the conotheca. This differentiation is absent in many early and later Belemnoidea (Belemnoteuthis, Phragmoteuthis, Diploconus), which in other structural elements are more closely related to the Teuthoidea and Sepioidea than the true belemnites.

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* In Acanthoteuthis speciosa there are at least 8 hook-bearing arms; Belemnoteuthis antiqua has certainly 10 such arms. The oldest type!

135 *Chapter 4*

SUBORDER TEUTHOIDEA*
Naef, 1916

Contents: a) Diagnosis. – b) Typical structure of the adult animal. – c) Typical postembryonic development. – d) Variation of the type of Teuthoidea.

a. DIAGNOSIS

Decapoda (p. 109) with rudimentary phragmocone which is often present only in the young stages as an unchambered spoon- to cone-shaped remnant ("conus") at the posterior end of the gladius, i. e. of the not calcified but well preserved proostracums in recent forms. Funnel incision of ventral mantle margin delimited laterally by distinct and usually sharply projecting angles. Gill axis with a wide longitudinal canal between the afferent and efferent vessels and connected with the mantle cavity between the branchial lamellae. Middle row of radular teeth always tricuspid, adjacent lateral rows bicuspid with a smaller cusp lateral to the main cusp. Nektonic animals ("permanent swimmers").**

b. TYPICAL STRUCTURE OF THE ADULT ANIMAL

The ideal or hypothetical ancestral form of the recent and fossil Teuthoidea will be named Prototeuthis. Its habitus is assumed to be Loligo-like, but this type differs from the Belemnoidea and the ideal form Metadecapus (p. 127) in the condition of the phragmocone, which is reduced to a rudiment, but situated in the typical place. The phragmocone or cone has the form (Figure 53) of an unchambered† (in recent species also non-
136 calcified) conical appendage at the posterior end of the proostracum which

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[*] Loligo-like. I established the group, but I have characterized it only by the species included (1916) and in a lecture given in 1917

[**] [Addition to the diagnosis of Teuthoidea: the family Enoploteuthidae is unique in that all radular teeth are unicuspid as in the Sepioidea. Only Enoploteuthis is normal (cf. Figure 146).]

[†] According to Hoyle (1886), Gonatus fabricii (q.v.) still has a phragmocone-like filling in the cone, apparently like the fossil Teuthoidea. In other recent forms I found at least a deposition of shell substance in the cone. These remains, however, have not been sufficiently studied and no definite interpretation can be given.

The reduction of the phragmocone in the Teuthoidea is surprising because this structure is the most ancient and most highly organized part of the shell. For a better understanding, it is necessary to point out that such a reduction already begins in the Belemnoidea, namely in the early (Triassic) Aulacoceratidae, e.g. Calliconites Gemm. in which the phragmocone consists mainly of the living chamber and only a few air chambers.

thus becomes the main part of the shell. The appendage will be named the cone, and the modified shell the gladius (Figure 54).

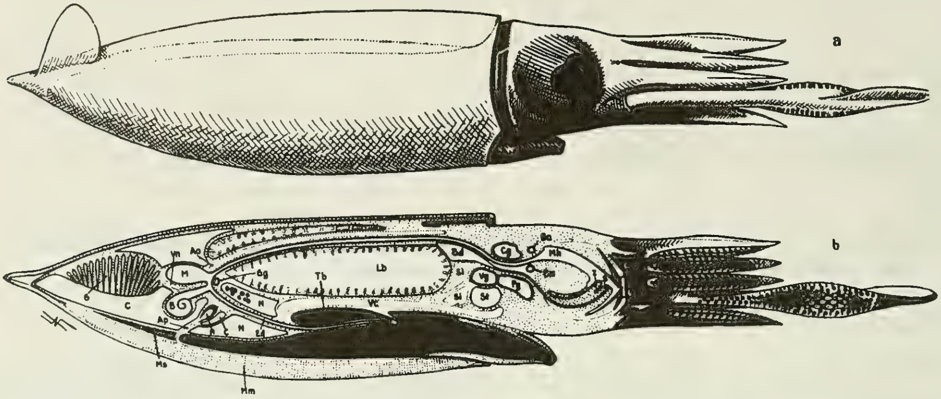

FIGURE 53. Lateral view (a) and median section (b) of Prototeuthis. Compare the relationships between shell, muscular mantle and fins with those illustrated in Figures 23 and 37. Note the form of the mantle margin, the neck folds, the condition of the arm apparatus, the position of the soft parts, especially of the median pallial septum and the mantle cavity with respect to the cone. Abbreviations as in Figure 37 (p. 110). Some typical blood vessels are shown: Vn — genital vein; Si — venous sinus. According to my present knowledge, the cone should be shown at least twice as long, i.e. its free margin displaced anteriorly so that the fin should be attached on its outer side (cf. Figure 66).

(137)

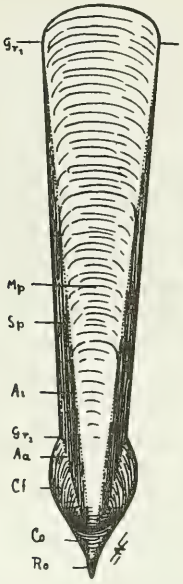

FIGURE 54. Shell of Prototeuthis, drawn on the basis of recent studies of fossil and living gladii of Teuthoidea. [Figure 58 (p. 141) is to be modified in the same sense.] The following elements are shown:

1 — proostracum with middle (Mp) and lateral (Sp) plates; 2 — cone which consists of ventral wall (Co), cone, cone flag and rostrum (Ro); Gr_1 — boundary between the growth margin of the middle and lateral plates at the end of the inner asymptote (Ai); Gr_2 — boundary between the growth margin of the lateral plate and cone flag at the end of the outer asymptote (Aa). This shell shows, slightly simplified, the conditions in Geoteuthis sagittata (Münster, Contribution No. 6, Plate VII, Figure 2) or in Loliginites sagittatus (Quenstedt, "Cephalopoden," Plates XXXV and XXXVI).

In recent species, the outer side of the cone bears stratified cartilage-like deposits, which are remains of the sheath and continue in a rudimentary rostrum. It may, therefore, be assumed that the Teuthoidea have to be derived from true belemnites or Aulacoceratidae, especially in view of the assumption (cf. Abel, 1916) that the belemnites had only 6 arms, like the typical juvenile stages of Oegopsida (q. v.) — i. e. like most of the known Teuthoidea (see footnote on p. 133). It should be considered, however, that there may be a great difference between a rostrum in general and a true belemnite spine. This is certainly true of the rostrum of the Teuthoidea (Gonatidae, Onychoteuthidae, Alloteuthis; q. v.). In these forms the rostrum is a pointed, fibrous process, strongly compressed laterally and usually situated dorsally on the cone. In profile, this is visible in the characteristic fan-like arranged lines which radiate from the apex of the cone (cf. illustration in Chapter 6).*

137 The proostracum consists typically of middle and lateral plates (p. 113), which are, however, indistinct in many Teuthoidea. Likewise, the division between lateral plates and cone may be even more indistinct than the Belemnoidea (Figure 40), which I do not assume for the ancestral form. In principle, we shall have to distinguish between middle plate, lateral plate, cone, septum and rostrum, in the analysis of a shell of Teuthoidea, provided that some of these parts are not reduced.

The inner asymptote lines are assumed to pass between the median and lateral plates and the outer asymptote lines between the lateral plate and the cone which separate zones of different growth (Figure 54; cf. p. 104).

The lateral and dorsal parts of the conotheca, i. e. the lamellae which form the cone, extend slightly anteriorly and form a spoonlike widening of the shell margin which is of particular importance for the modification of the gladius (p. 142). These parts do not differ otherwise from the rest of the cone and pass without boundary into its ventral wall. I call them cone flags for the Oegopsida, according to Pfeffer (1911).

Figure 35 shows that the reduction of the phragmocone results in an increase of the muscular mantle. Another associated process is the reduction of the heavy sheath and of the rostrum, the function of which is partial compensation for the increased buoyancy of the posterior end caused by the air chambers (p. 110). Ecologically, such a modification can be interpreted as the shedding of a cumbersome and complex hydrostatic apparatus the
138 function of which is replaced by active organs — muscles — instead of passive swimming and protective devices. Undoubtedly a progress, this change explains the supplantation of the older belemnoid type by the more advanced teuthoid type, which occupies a dominant position among the recent marine invertebrates.

Like the recent Loliginidae derived from it, Prototeuthis is assumed to be an actively and permanently swimming animal. (Recent Teuthoidea never descend to the ground; there are no benthic forms among them, as far as is known.) However, another interpretation is also possible. Some of the most ancient Teuthoidea of the shallow Liassic sea were plump, with a heavy shell and a huge ink sac; examples are Geoteuthis bollensis and Belemnosepia lata from the Lower Liassic (E) of the Swabian Jurassic (Figure 144). These forms could be assumed to have had a Sepia-like mode of life, and the reduction of the phragmocone and rostrum (p. 110) could be explained ecologically as a loss of the hydrostatic devices, which were necessary for a nectonic life.

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* Only exceptionally observed in the Belemnoidea, but in forms which can be regarded as closer relatives of the Teuthoidea, according to the above (cf. Aulacoceras in Abel, 1916, p. 131, Figure 54).

Figure 55 gives a general orientation of the phylogenesis of the Teuthoidea (or their derivation from the typical decapod structure) and shows the essential changes in a series of ideal juvenile stages. In contrast to the preceding description, a flag is assumed to exist already on the gladius of such an early form as Prototeuthis (cf. p. 146). This flag results from a change of form and stronger development of the lateral plates, and is therefore homologous to them.

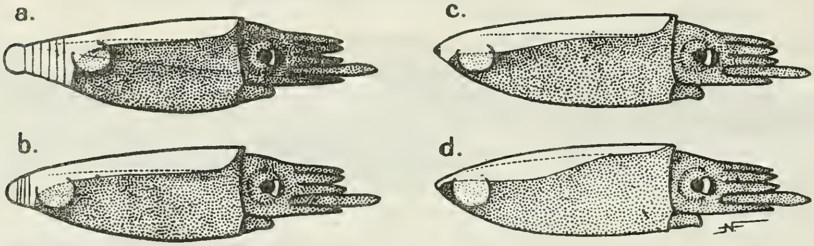

FIGURE 55. Diagrams of the derivation of Teuthoidea. Shown are 4 young Decapoda.

a — Protodecapus; b — transitional stage; c — Prototeuthis; d — Metateuthis (see below). The reduction of the phragmocone results in an expansion of the muscular mantle and viscera toward the posterior end. The rostrum is still absent in these stages, also if it develops later (see p. 108).

Because of the reduction of the phragmocone, the fins are situated close to the posterior end. The relatively narrow proostracum at the transition
139 to the cone brings the two fins closer to the dorsal median line without uniting them in the middle. They are also still very small in relation to recent fins, although they have the same rounded-triangular form with an anterior indentation, which forms an "earlobe" (Figure 53). The articulation with the body, i. e. with the conus part of the shell, resembles that of Protodecapus (p. 114), but the capsule of the articulation is completely separated from the shell sac (Figure 56).

A special character of all Teuthoidea is the form of the mantle margin, which forms sharp, markedly projecting angles on each side of the funnel incision in contrast to the rounded angles of most Sepioidea.

The arm apparatus of Prototeuthis shows the external characters inherited from Metadecapus (p. 127), at least in the juvenile stages. The arms and tentacles bear, respectively, 4 and 8 rows of suckers. Of these, the two median rows on the arms and part of the 4 median rows on the marginal part of the tentacle club develop into hooked suckers and true hooks (p. 133). Swimming and protective margins are developed as in Protodecapus and Metadecapus (Figure 51). The tentacle pockets have developed further: in the Teuthoidea, they penetrate posteriorly between the muscular organs of the head, and separate them from each other. This change, however, may have been only slightly indicated in Prototeuthis. The basal parts of the tentacles can be hidden inside the pockets as far as they are able to contract, but a larger part of the tentacle cannot be accommodated in them as in Sepia (q.v.). Here too, the tentacles are extended straight anteriorly when at rest. The tentacles of Prototeuthis have the same function as those of Protodecapus (p. 119).

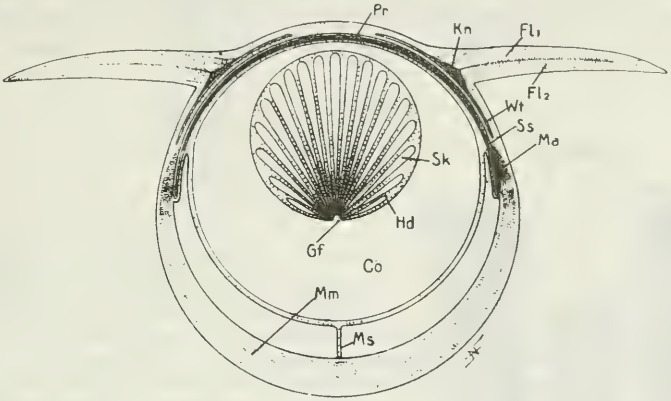

FIGURE 56. Cross section of the fin area of Prototeuthis. Compare with Figures 26 and 41. The capsule of the fin base is completely separated from the shell sac, and the insertion of the muscular mantle is displaced to the outer side, i.e. to the lateral plate of the proostracum (see Chapter 5). As a result, the shell margin projects into the mantle cavity, forming an edge:

Pr — proostracum; Kn — fin cartilage; Fl_1 — fin musculature, upper layer; Fl_2 — fin musculature, lower layer; Wt — capsule of fin base; Ss — shell sac; Ma — attachment of the muscular mantle; Sk — sperm tubules; Hd — testis; Gf — groovelike opening of the testis; Cö — coelom; Ms — mantle septum; Mm — muscular mantle.

140 While the arm apparatus adds little to the characterization of Prototeuthis, the outer side of the head shows some distinctive characters, i. e. the neck (the name does not fit the anatomical character of the region) with a system of edgelike elevations ("neck edges") on each side, namely two transverse edges, one anterior and one posterior, connected by 4 longitudinal ridges (Figure 53). The third longitudinal ridge (counting from above) bears the olfactory organ on the dorsal side at the junction with the posterior transverse edge, so that the olfactory organ projects more from the head. The anterior transverse edge continues dorsally beyond the beginning of the longitudinal edges and ends ventrally in a strongly projecting "cheek tubercle" which is situated in the angle in which the anterior transverse edge meets the ventral (fourth) longitudinal edge and the arc-shaped funnel edge. The latter surrounds the funnel pit, which is a depression on the ventral side of the head in which the protruding part of the funnel is situated. All these elevations are formed by the arrangement of muscle tissue in the subcutis; they may be absent or form conspicuous ridges (Plate II, Figure 1).

The eye resembles that of Protodecapus (p. 115).

The characters of the organs of the mantle cavity, like those of the whole animal, are caused by the transformation of the shell, and follow the shell pattern automatically. The reduction of the phragmocone causes a corresponding change

141 of the muscular mantle and the posterior part of the abdominal complex, which advance posteriorly as the cone becomes smaller. The mantle sac thus assumes the general form characteristic for the Loliginidae and Oegopsida, and which we assume for Prototeuthis (Figure 53). The posterior pallial arteries and veins, the musculus rectus abdominis and the fin nerves, which pass along the margin of the proostracum, become thus markedly lengthened.

(140)

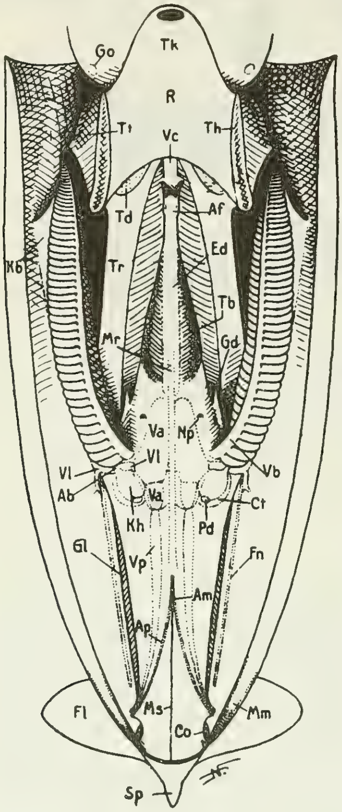

FIGURE 57. Situs of mantle cavity of Prototeuthis after removal of the ventral part of the muscular mantle and slight extension in the normal body position. The funnel apparatus is still as in Protodecapus as are the funnel retractors (Tr), gills (as far as visible), anus (Af), intestine (Ed), ink sac (Tb), renal (Np) and genital papillae (Gd), the translucent venous appendages (Va) and branchial hearts (Kh), the musculus rectus abdominis (Mr), the lateral pallial veins (Vl), the margin of the posterior part of the proostracum (Gl) and the adjacent nerves of the fins (Fn). Reduction of the phragmocone results in an advance of the muscular mantle (Mm) and viscera towards the posterior end with a corresponding lengthening of the posterior pallial arteries and veins (Vp), of the nerves of the fins (Fn), and the entire posterior abdominal complex. Also important are the characteristic form and position of the fins (Fl) and the funnel gland (Td), parts of which extend back toward the infundibular retractors.

Go – olfactory organ; R – funnel; Tt – funnel pocket; Th – funnel bond; Vc – vena cava; Kb – branchial attachment; Vb – branchial vein; Ab – branchial artery; Pd – pericardial gland; Ct – coelom pocket for the branchial heart; Am – median pallial artery; Ms – mantle septum; Co – cone; Sp – rostrum.

The animal is assumed to be a male, but the opening of the genital pocket from which the genital process projects (Gd) is not shown (cf. Figure 35).

Removal of the viscera and cutting of the branchial attachments and mantle vessels at the margin of the muscular mantle results in the condition shown in Figure 58, which clearly illustrates the typical characters of the shell and the correlation between the soft body and the shell.

The development of the genitalia, the sexual dimorphism and hectocotylization are the same as in Protodibranchus and Protodecapus (pp. 104 and 126). Jaws and radula (p. 122) also show no special characters.

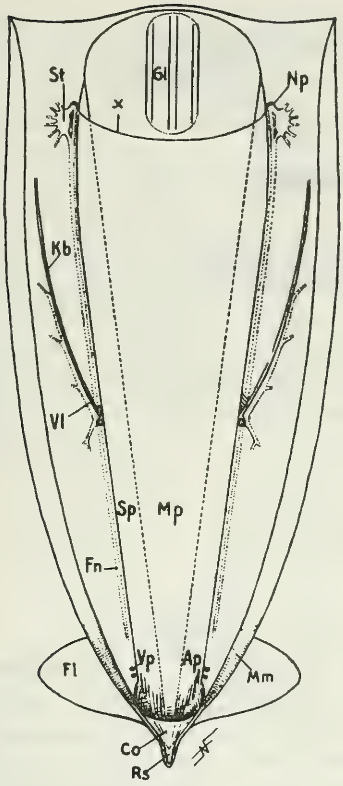

FIGURE 58. Situs of shell of Prototeuthis, after removal of viscera. Compare with Figure 34; note the general similarity, and also the differences resulting from the reduction of the phragmocone:

Gl — collar bond (gliding surfaces); Np — pallial nerve; St — stellar ganglion; x — posterior boundary of the dorsal mantle cavity; Kb — insertion of branchial attachment; Vl — lateral pallial vein; Mp — median plate; Sp — lateral plate of the gladius; Fn — nerve of fin; Vp — posterior pallial vein, point of entry into the mantle; Ap — posterior pallial artery; Fl — fins; Mm — muscular mantle; Co — cone; Rs — rostrum.

c. TYPICAL POSTEMBRYONIC DEVELOPMENT

Like the general organization, the development of the Loligo-like Decapoda appears to be influenced markedly by the shell. In all other respects, there is a marked resemblance to the Sepioidea throughout the whole embryonic period, as will be described in Volume II (Loligo-Sepia); there are at first only few differences between the two suborders also in the postembryonic stages (cf. Figure 59 with the corresponding figures in Chapter 37).

142 The reduction of the phragmocone in the systematic (or phylogenetic) sequence of steps is expressed ontogenetically at an early stage (Figure 59a), in that the cone part of the shell becomes relatively reduced (cf. Chapter 5, Figure 66) and does not become separated from the proostracum to form an inflated embryonic chamber.* A siphuncle probably develops later (cf. Loligo, Chapter 6; Figure 59d), and incompletely differentiated septa may still be formed. However, forms which could have given information on this subject (very young, primitive Oegopsida, especially Gonatus) were not available.

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* Since the formation of the embryonic chamber of Spirula is not known in detail, it is possible to assume that at first the soft embryonic chamber becomes inflated and vesicular only after its closure, when it is filled with air (cf. footnotes on p. 88). Calcification could take place later from the outside. But compare Orthoceras, p. 88.

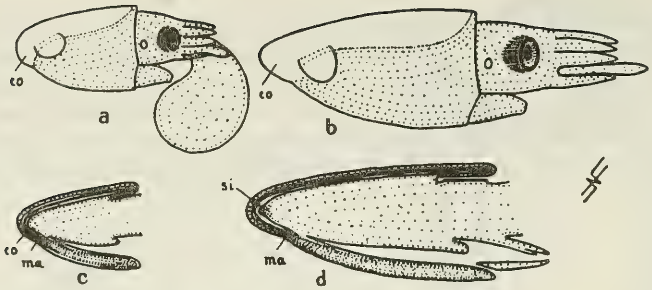

FIGURE 59. Embryo (a, c) and early young stage (b, d) of Prototeuthis:

a and b – lateral aspects with translucent shell,showing the attachment of the muscular mantle; c and d – median sections. Compare the relationships shown here with those of Figure 36. co – cone; si – rudimentary siphuncle; ma – attachment of the muscular mantle.

For details see Protodibranchus (p. 107).

d. VARIATION OF THE TYPE OF TEUTHOIDEA

To the Teuthoidea belong a number of fossil genera (see below) which closely resemble the idealized Prototeuthis. They have in common with Prototeuthis the form of the median plate of the gladius (p. 137), which widens anteriorly into a wide, slightly variable curve. This causes the lateral position of the stellate ganglions, taken over from the typical Decapoda (Belemnoidea) but never observed in the recent Teuthoidea, and the form of the muscular mantle, which necessarily affects the manner of movement. Other anatomical differences are necessarily connected with it (see p. 146).

These forms had a moderately convex, strongly calcified gladius without a sharply projecting, ventrally groove-shaped median keel. They apparently had a large, pointed cone. I have named them Prototeuthoidea because of their close relations to the Belemnoidea.

Prototeuthoidea (nov.) (= Loliginites tenuicarinati Quenstedt)

Diagnosis: Fossil Teuthoidea (Liassic to Cretaceous) in which the median
143 plate of the strongly calcified gladius* is usually sharply delimited by asymptotes, and the gladius very blunt anteriorly and at least half as wide as the mantle sac; lower side of middle plate without a median keel which is gutter-shaped ventrally (Figure 62), but instead at most with solid supporting ridges which become reduced or disappear anteriorly.

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* It is difficult to determine the degree of primary calcification of fossil shells embedded in calcareous material; the very delicate growing marginal parts are almost never preserved. As in Sepia (q. v.), they were probably not calcified. Calcification takes place as in all molluscs by the subsequent deposition of crystallized CaC_{03} in the conchiolin layers.

I place in the Prototeuthoidea, pending a definitive systematic treatment of all fossil shells, the following 3 families except for some doubtful forms:

1. Leptoteuthidae (p. 47). Fossil shells illustrated in Figures 54 and 60, especially the genera Leptoteuthis H. v. Mayer and Plesioteuthis Wagner, which have a tripartite median plate, a spoon-shaped cone flag and a conical conus.

2. Geoteuthidae Naef.* Here belong forms like Belopeltis simplex Voltz (= Geoteuthis lata Münst. = Belemnosepia lata Orb., etc. Cone flag wide, leaf-shaped, occupying about the posterior half of the gladius (Figure 6).

3. Belopeltidae.* Fossil shells of the type of "Loligo" aalensis Zieten.* Cone flag leaf-shaped, almost reaching the anterior end and separated 144 from the median plate by narrow areas with angular stripes projecting anteriorly and posteriorly. Ink sac very large (as in the Leptoteuthidae) and situated far posteriorly. Loliginites coriaceous Quenstedt also belongs here.

(143)

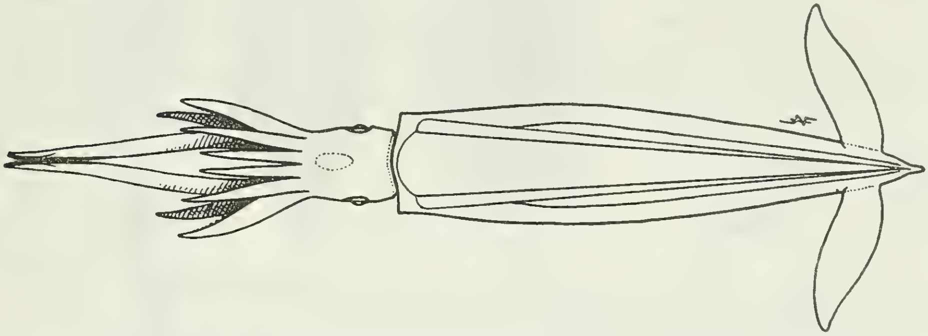

FIGURE 60. Reconstruction of a Prototeuthoid after a photograph by Crick (1915) of a plate from the lithographic slates of Eichstätt ($^1/_4$ natural size). The gladius has a wide, tripartite median plate and weakly developed lateral plates. The rostrum is distinctly compressed. The fins are very wide, short, subterminal. Compare with the similar illustration in Zittel-Broili (1915, p. 583). The cone flag is not visible (cf. Figure 57 on p.137). The animal drawn here is named by Crick Plesioteuthis prisca Rüpp.** This species, of which I have compared at least 30 specimens, is actually much more slender, particularly the median plate of the gladius is only about half as wide. The fins are smaller. The general form of the shell is that of the genus Leptoteuthis H.v.M. In the known species of this genus, however, the median plate is much wider (L. gigas A. Wagner, L. alatus Fraas, which is probably identical with gigas). The particularly well preserved fossil represents a new species of Leptoteuthis (sagittata Naef) which resembles the related Plesioteuthis; the narrow median and lateral plates are characteristic for this species (cf. my Fossile Cephalopoden).

The Prototeuthoidea are closely related to the Belemnoidea, but shells leading gradually to the recent Metateuthoidea occur already in the Liassic.

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* [According to corrections on p. 147, read Geoteuthidae Naef, instead of Belemnosepiidae; "Loligo" aalensis Zieten instead of Geoteuthis bollensis; Belopeltidae instead of Geoteuthidae. About Plesioteuthidae see p. 147.]

** [A repeated examination of Crick's figure shows that this "Plesioteuthis prisca" is actually Leptoteuthis gigas. The width (angle) of the median plate increases during development and should show the relationships in such small specimens. The lateral plates are much wider here than in my figure and therefore resemble those of Leptoteuthis gigas.]

This transition is expressed in the following characters: 1. The gladius becomes less calcified, hornlike, thin and apparently elastic. 2. The anterior end of the gladius becomes narrower and tapers into a more or less sharp point (Beloteuthis) or into a narrow process (Teuthopsis), which causes anatomical displacements in the area of the neck cartilage, the origin of the cephalopodial retractors and the stellate ganglia (see next chapter). 3. This anterior narrowing is caused by the narrowing of the entire median plate (p. 146), which becomes a narrow stripe between the large, leaflike lateral plates. This median plate resembles the midrib of a leaf and is named "rhachis," while the lateral plates become connected with the well developed cone "flag" and form a larger flag together with it (Figure 62).

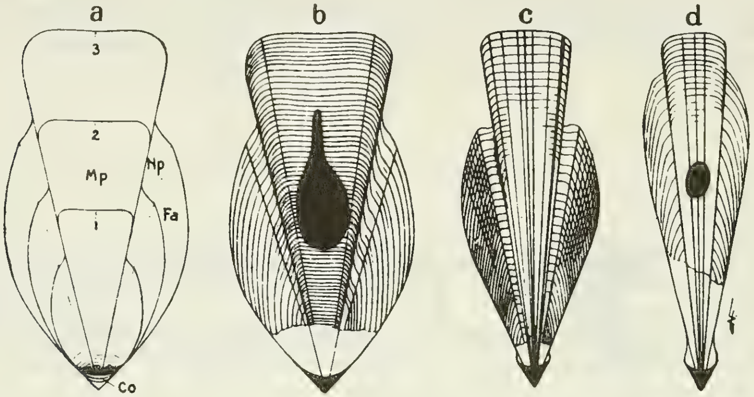

FIGURE 61. Shells of fossil Belemnosepiidae [Geoteuthidae] after Orbigny, 1855:

a and b — Geoteuthis ("Belopeltis") simplex (Voltz 1840); c — Parabelopeltis ("Geoteuthis") flexuosa; d — Loliginites coriaceous Quenst. 1849. The animals are assumed to be Sepial-like, i.e. plump and heavy. Note the huge ink sac. The conical conus is added hypothetically in all three species; the cones of all three species should look alike, including d, provided that this belongs to this group and is not an arbitrarily reconstructed form (Leptoteuthis?). The anterior ends are also reconstructed (by d'Orbigny), and his drawings are inaccurate. The lateral plates, in b and c, for example, which are narrow, have disappeared (cf. Figure 54). The leaflike widening of this shell is actually a cone flag.
a — diagram based on my own experience for the analysis of b; 1, 2, 3 — three stages of growth, according to the growth lines; Mp — median plate; Np, Fa — differentiated parts of the cone flag; Co — cone.

4. The lateral plates are widened only in the posterior part of the shell, while they taper anteriorly. As a result, the anterior end of the rhachis is more or less free (see also (Figure 60). This step is achieved by a number
145 of transitional stages in the Beloteuthidae.* 5. The rhachis is curved ventrally into a groove, forming a large dorsal keel, while the lateral plates retain their shallow, curved primary form. 6. The cone becomes rounded, spoon- or scooplike.

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* All these forms and their relatives lack distinct asymptotes between the median and lateral plates of the proostracum which is caused by the form of the anterior end. A sharp bend (as in Gr_1, Figure 54) is absent here at the growth margin.

These changes lead to the recent types of Teuthoidea, i. e. the Metateuthoidea. The fossil forms from which the Metateuthoidea can be derived (p. 47) are named Mesoteuthoidea.

Mesoteuthoidea (=Loliginites crassicarinati Quenstedt)

Diagnosis: Fossil Teuthoidea (Liassic to Cretaceous) with the median plate of the proostracum tapering anteriorly into an arc, apex or pointed process and bent more or less distinctly into a groove (keel) which is open ventrally, and not delimited sharply by asymptotes between the median plate and the lateral plates. Cone flag large, occupying about half the length of the gladius and passing posteriorly into the spoon- or scoop-shaped cone. Outer asymptotes marked clearly but not sharply by a slight bend of the growth lines. Four families (p. 47) are listed below.

1. Trachyteuthidae. Plump Teuthoidea with Sepia-like shell, which is strongly calcified, with a zone of tubercles along the middle of the dorsal side. Median plate of proostracum still relatively wide, ending anteriorly in a rather blunt arc (Figure 62, Chapter 4), without distinct keel. (Trachyteuthis hastiformis Rüpp. from the Solnhofen slates, and related species. (Cf. Zittel-Broili, 1915, p. 582, Figure 1, 273.)

(146)

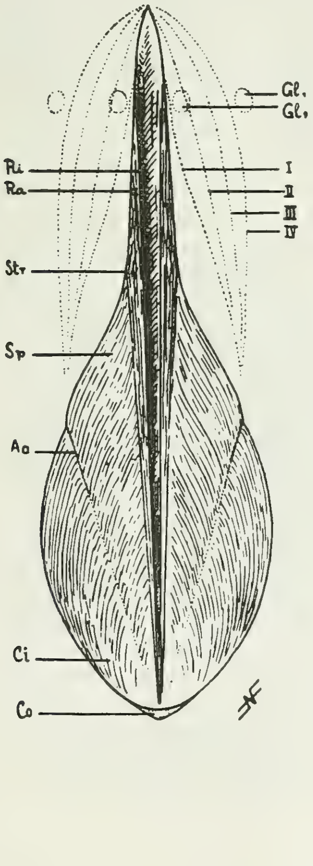


FIGURE 62. Shell of Palaeololigo Naef = Teuthopsis oblonga Wagner (= T. princeps Wagner), reconstructed after the original in the Munich paleontological collection and by comparison with well preserved fossils from Solnhofen. Eichstädt and Daiting. Note the spoonlike cone (Co) and the leaflike lateral plates (Sp) which are connected with the similar halves of the cone flag (Ct) to form the flag:

Ra — free rhachis (the lateral boundary of the median plate is shown) passing into the lateral plates by a longitudinally striped zone (Str); Aa — outer asymptote dividing the proostracum from the cone flag. (This boundary is always distinct also in recent gladii with a well developed flag.) The shell illustrated here is related and obviously transitional to the Metateuthoidea. This form and the family it represents would be isolated among the Metateuthoidea; they are therefore placed with their fossil relatives which they resemble most closely. The dotted lines show diagrammatically the outline of the proostracum in four related species which represent successive steps of the described (p. 144) metamorphosis within the Mesoteuthoidea; I—Beloteuthis acuta (see below), closely related to Palaeololigo; II—"Loligo" aalensis; III—Beloteuthis subcostata; IV—Trachyteuthis hastiformis, which still resembles the Prototeuthoidea (Figure 61). Gl_1 — the hypothetical position of the stellate ganglion in this species; Gl_2—the corresponding place in Palaeololigo aalensis (cf. the corresponding figures in Chapter 6).

2. Beloteuthidae. Plump Teuthoidea with a leaflike shell, already Loligo-like, smooth, less calcified, with a large median keel and with a blunt, sharp or slightly produced anterior end. Beloteuthis Münst. and related forms from the Liassic (Figure 62, III, II, I).

3. Palaeololiginidae. Slightly more slender Teuthoidea with completely Loligo-like shell, ending anteriorly in a long "free rhachis." posteriorly with a leaflike flag consisting of cone flag and the lateral plates (Figure 62, p. 146). Palaeololigo Naef, 1921 = Teuthopsis Wagner from the Solnhofen slates (Malm) and similar forms from the Lower Cretaceous of Lebanon.

4. Kelaenidae. (Cf. p. 47). This very interesting, aberrant group does not show any relationship to the recent types. Kelaeno Münst. of the lithographic slates of Bavaria and Württemberg.

Figure 62 illustrates the derivation of a Loligo (Metateuthis)-like shell; only the significance of this metamorphosis for the organism and some details and relationships are discussed here.

146 As its anterior end becomes more pointed, the proostracum becomes necessarily narrower in favor of the lateral plates; the more pointed the shell becomes, the narrower becomes the growing margin between the stellate ganglia (which are closely approximated laterally, see Figure 58) from which the proostracum is formed. This process also results in a narrowing of the neck bond and a weakening of the part of the gladius which supports the anterior part of the mantle sac. The narrowed anterior end of the gladius (Figure 62) is attached to the neck and forms alone the "backbone" for the entire posterior part of the body. It also separates the two stellate ganglia and the lateral halves of the muscular mantle. Some differentiations must develop by compensation: the rhachis becomes stiffened by becoming thicker and bending into a keel, thus forming a new structure outside the complex of parts, which justifies the designation taken from the morphology of recent Decapoda. As a result, the lateral plates are pressed against the cone flag, to which they become connected to form a flag. The heterogeneous origin of this flag is evident in its structure, despite its superficially uniform appearance.

I realized this process only recently. My early view, partly erroneous and partly speculative, is expressed in Figures 55c, d and 61c, d. which could not be substituted subsequently. My present morphological concept is illustrated in Figure 62, which should be compared with Figure 54.

147 A more detailed treatment of the morphological concept will be found in my book on the fossil Cephalopoda. It should be mentioned here only that the Trachyteuthis-like forms (p. 145), Beloteuthis subcostata Münst., "Loligo" aalensis Zieten and B. acuta Münst., form a series which leads to Palaeololigo. This statement should be made here because the available illustrations are of the above species, although under a confusing variety of names.

149 *Chapter 5*

SERIES METATEUTHOIDEA
Naef, 1921 (System p. 535)

Contents: a. Diagnosis. b. Establishment of the group. c. Typical structure of the adult animal (p.155). d. Typical postembryonic development (p.160). e. Variation of the type of the Metateuthoidea, with an appendix of the Metateuthoidea myopsida (p. 165).

a. DIAGNOSIS

Recent Teuthoidea (p. 135). Gladius with a distinctly strengthened median "rhachis," which is usually grooved ventrally and keeled dorsally, with almost free anterior part, accompanied posteriorly by a leaf-shaped "flag" which passes terminally into a spoon-shaped or conical "conus," at least in early youth. Buccal pockets very deep, together forming a slit which surrounds the pharynx, the 6 parts of which are separated only by narrow septa or are contiguous at the bottom. Strictly nektonic mode of life ("permanent swimmers"). Eggs numerous (at least 4) connected in a gelatinous mass.

b. ESTABLISHMENT OF THE GROUP

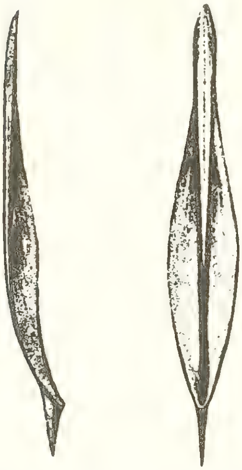
As stated on p. 47, the Metateuthoidea include the Oegopsida d'Orbigny, the Loliginidae, and the related recent genera Promachoteuthis Hoyle and Lepidoteuthis Joubin. The latter two genera are only incompletely known, and are more or less closely related to the Loliginidae in structure.

I recognized the closer relationship between the Loliginidae and the Oegopsida from a cursory examination of these groups which also suggested that the placing of the Loliginidae together with the Sepiidae, Sepiolidae, etc. would be artificial. The suborder Myopsida and its position opposite the Oegopsida (d'Orbigny 1845) therefore becomes untenable.

However, a more detailed examination reawakened my uncertainty. Numerous facts made orientation difficult, and I therefore refrained from a systematic revision (see Naef, 1912). I could not ignore the fact that the Loliginidae share with the other "Myopsida" (Sepioidea of the present
150 classification) a number of striking characters which separate them from the "Oegopsida." A number of extensive convergences between Sepia and Loligo would have to be accepted if a closer relationship between these genera were to be denied. I later separated the Loliginidae and their problematical appendix (Promachoteuthis and Lepidoteuthis) as "Loliginiformes" from the "Sepiaeformes" within the "Myopsida" (Naef, 1913, p. 461).

I had to abandon this preliminary solution, mainly following paleontological studies (see Chapters 38 and 40) which clarified the nature of the Sepia-like Decapoda and the marked contrast between the Loligo and the Sepia type. This led to the establishment of the Teuthoidea in contrast to the Sepioidea (cf. Naef, 1916, 1921), which will be explained here in detail. Although this distinction is based on very marked typical differences (cf. Chapter 38), the traditional character of d'Orbigny's classification into Oegopsida and Myopsida makes a more thorough discussion of these groups necessary. D'Orbigny's classification has been generally accepted and plays an important part in the literature, where general morphological or historical relationships are discussed. The question whether the Oegopsida or Myopsida are the primitive Decapoda has become almost a joke (cf., for example, Chun, 1910, Spirula, and Naef, 1911). This question can naturally not be answered at present, although it is a paleontological fact that the Teuthoidea are much more ancient than the Sepioidea. The Teuthoidea occur already in the early Mesozoic (lower Liassic) and reach the characteristic Loligo type in the upper Malm (p. 146). The Sepioidea (q. v.), on the other hand, are known only from the Paleocene.

The shell of Loligo can therefore not be considered to have developed by simple reduction from a Sepia-like shell. Neither is the reverse acceptable. The main character of the Loligo-like shell is the rudimentary phragmocone (p. 135), under retention of the typical proportions. The Sepioidea, on the other hand, have a well developed chambered shell with septa and a siphuncle, but with a markedly different topography and correlations (Chapter 38). Both Teuthoidea and Sepioidea have developed from the main or central group of the Belemnoidea (p. 16), or from the common type of the Decapoda. However, the Teuthoidea diverged from the Belemnoidea much earlier than the Sepioidea (cf. also Naef, 1922, Die fossilen Tintenfische, G. Fischer, Jena*).



151 FIGURE 63. Gladius of a typical species of Metateuthoidea (Teleoteuthis intermedia Pfeffer). 3×. The median rhachis is bordered by dark lines and has a groove-like depression. Also visible are the leaf-shaped flag and the small terminal cone with the dorsally attached rostrum.

D'Orbigny's classification has therefore definitely to be discarded, together with the classification of the Decapoda in general. However, we have to discuss in greater detail the characteristics of the "Myopsida," from which we intend to transfer a large number of species to the new group described here. Many renowned authors accepted the unification of the Loligo and Sepia types, and I was reluctant to abandon this early classification. There must therefore be strong reasons, valid or apparent, for this which will have to be thoroughly examined and discussed, including anatomical and embryological data. Reference to the literature are given for well known facts; if new data are given, the reader is referred to later parts of this monograph (Vols. II and III).

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* This publication contains a revised interpretation of the common type of Decapoda (illustrated especially in Figure 62) on the basis of important recent data. See also Concluding Chapter I of this monograph.

Characterization of the "Myopsida" d'Orb. 1845

1. All "Myopsida" (except Spirula; cf. Chun, 1910), i.e. the Sepioidea and Loliginidae close the orbits by a definitive contraction of the primary lid ("corneal fold"), which later forms a tough, transparent skin ("cornea") which covers the pupil permanently (cf. Oegopsida, Chapter 9). This is the main character of the group.

2. In all "Myopsida" the genital duct is developed only on the left side. The Oegopsida, on the other hand, usually have at least a paired oviduct (except Pyroteuthis), sometimes (Calliteuthis) also a paired sperm duct.

3. All "Myopsida" have accessory nidamental glands. The Oegopsida lack these glands, as far as is known (but see Ctenopteryx, Chapter 11).

4. All "Myopsida" have a similar embryonic development which differs markedly from that of the Oegopsida. The embryos of the "Myopsida" have an external yolk sac, which is (almost) absent in the Oegopsida; the arm "anlagen" of the "Myopsida" develop almost simultaneously, while the latero-ventral and ventral arms of the Oegopsida develop later, usually post-embryonally, and the animals therefore hatch with only 6 arms including the tentacles.

152 5. Most "Myopsida" show a similar sexual dimorphism, mainly in that the spermatophores are attached to the buccal funnel of the female and the left ventral arm is used in copulation in most cases.

6. Most "Myopsida" (Spirula?) have a similar ecology; they are more or less benthic and coastal forms. The Oegopsida, on the other hand, are strictly nektonic inhabitants of the open, deep sea, independent of the bottom to a large extent.

7. All "Myopsida" lay their eggs at the bottom, on solid substrates. The Oegopsida produce planktonic eggs, as far as is known.

8. The true genus of Sepioidea "Idiosepius" closely resembles young Loliginidae to such an extent that Joubin (1894, Céphalop. d'Amboine) described a specimen of this genus as a new species of Loligo (cf. Figure 275 and Plate I).

9. The "Myopsida" are anatomically uniform and different from the Oegopsida. Only two characters will be mentioned: a) in the Myopsida, the vena cava divides into two venous branches dorsal to the hind intestine, while the branching is apparently always ventral in the Oegopsida; b) the genital artery of the Myopsida originates directly from the heart; it originates indirectly from the posterior aorta in the Oegopsida.

153 These characteristics seemed to justify d'Orbigny's classification sufficiently as long as no compelling evidence was produced against it. However, I had doubts early in my systematic studies, as to whether this classification is natural. The similarity in the general anatomical habitus of the Oegopsida and Loliginidae surprised me particularly. I therefore began to look for new objective data for the classification (cf. also Chapters 9 and 38). A new orientation resulted from the morphology of the shell, which made it possible to include the fossil species as well and resulted in the separation of the Sepioidea and Teuthoidea used here.* It became evident

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* The differences in the typical form of the shells are particularly important as they are connected with anatomical differences (Chapter 9).

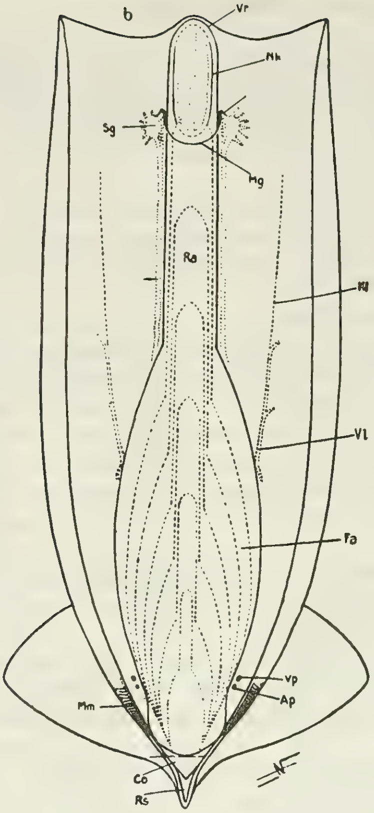

FIGURE 64. Correlation of the shell of Metateuthoidea to the soft parts (muscular mantle and adnexes), or shell situs (cf. pp. 124 and 141). The changes described on pp. 144 – 146 are illustrated here. In comparison with Figure 62, the relationships approximate the recent forms derived from this type: the cone flag is restricted to the posterior end and is atypically (and excessively) reduced in comparison to the lateral plates (Fa) so that the fins extend anteriorly beyond their primary position (cf. also Figure 65, which shows the typical relationships better):

Vr – growing anterior margin of rhachis (shown too blunt); Nk – collar bond; Sg – stellate ganglion; Mg – posterior boundary of dorsal mantle cavity, above it without letter, the cut pallial nerve; Ra – rhachis; Kl – attachment of gill band; Vl – lateral pallial vein; Fa – "flag" (lateral plate); Vp – point of entrance of posterior pallial vein; Ap – same of posterior pallial artery into the muscular mantle (Mm); Co – cone; Rs – rostrum.

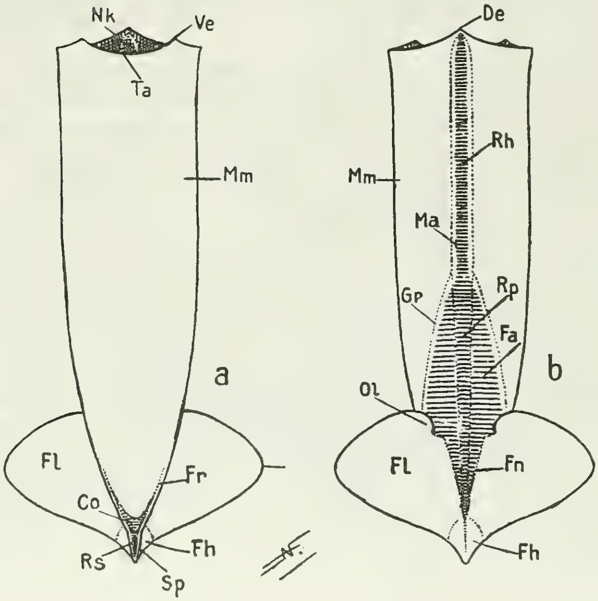

FIGURE 65. Mantle sac and fins of Metateuthis. Left – ventral, right dorsal. Note the outline of the mantle sac, fins, mantle margin; the form of the gladius can be reconstructed from the two figures:

Nk – neck bond; Ta – incision of funnel; Ve – ventral corner of mantle; De – dorsal corner of mantle; Mm – muscular mantle; Fl – fin; Fr – free margin of shell, ventral; Co – cone; Rs – rostrum; Fh – skin fold of fin; Sp – apex of body; Rh – rhachis; Ma – attachment of mantle to gladius; Gr – margin of gladius; Rp – posterior part of rhachis; Fa – flag; Ol – "ear lobes"; Fn – attachment of fin.

that the shell of Loliginidae had no place in the Sepioidea or in their close relatives. The shell proved that the Loliginidae were distinct Teuthoidea which, together with the Oegopsida, constitute the group of Metateuthoidea, in contrast to the fossil groups (pp. 142 — 145). The above facts made a revision necessary and led to the following conclusions.

1. The development of a "cornea" as defined above is no systematic character in itself. It is generally characteristic for forms living close to
154 the bottom, in contrast to nektonic animals which are not connected with the bottom or the shore. In the latter group, closure of the orbit appears unnecessary. This closure is not monotypic (i. e. monophyletically developed in the "Myopsida." It differs markedly in the different groups even within the Sepioidea (q. v.). The cornea of Sepia and Loligo, therefore, cannot form the basis for the establishment of a systematic group.* It is to be assumed that the ancestral forms of the Teuthoidea and Sepioidea had open orbits (primary lids).

2. In the juvenile stages the "anlage" of the genital duct is bilateral throughout (cf. also Döring, 1908), and it must therefore be assumed (p. 141), that the ancestral adult Decapoda also had a bilateral duct. Paired oviducts are present also in some adult "Myopsida" (Idiosepius), and unpaired ducts are found also among the Oegopsida (Pyroteuthinae). The majority does not decide (see p. 18 ff.).

3. Accessory nidamental glands (see Chapter 11, Plate III, Figure 2) are also ("still") present in the true Oegopsida (Ctenopteryx) and should be considered as primary in all Decapoda (p. 125).

4. The same interpretation is valid for the embryonic outer yolk sac of the Decapoda. Such a sac is present also in the Octopoda; the different structure of the arms, together with the reduction of the outer yolk sac and some other characteristics of the development of the Oegopsida are secondary, while the "Myopsida" retained the typical condition.

5. The attachment of the spermatophores in the buccal funnel is also the primary behavior in all Dibranchiata, since it closely resembles the behavior of Nautilus (p. 63; cf. p. 106). The left ventral arm, however, is often hectocotylized in the Oegopsida as well (cf. Illex) and probably represents the typical genital arm of the Decapoda.

6. Nektonic forms are also found among Sepioidea (Spirula). However, the Loliginidae are permanent swimmers which never rest on the bottom, although they live near the bottom or the shore. The resemblance to the Oegopsida is therefore more far reaching also in the mode of life.

7. Oviposition on the bottom is again the primary behavior (Nautilus, Octopoda, Sepioidea, Loliginidae); only the Oegopsida have pelagic eggs. (The eggs of Argonauta and Tremoctopus are also deposited on a solid dead body, even if this is carried along.) On the other hand, the eggs of Sepioidea are deposited singly, those of Loliginidae and Oegopsida are deposited primarily in formed, gelatinous masses containing several to many eggs (p. 149).

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* The development of Sepia and Loligo (Vol. II, Plates VI, XIX) is also quite different, but the differences cannot be formulated in brief terms. This is, however, possible in the Sepioidea (cf. the diagnosis of Spirula, Chapter 39; Sepiidae, Chapter 40; Sepiolidae, Chapter 42). It is difficult to define structures in the same position (homologous structures) as typically similar or not similar. Compare the terms homoplastic and homogenetic in Lankester (1870).

155 8. Idiosepius is, as far as is known, not a transitional form between the Sepioidea and Loliginidae. The similarity of habitus of Idiosepius with that of young Loliginidae is not specific; young Oegopsida show the same habitus, which is typical for young Decapoda in general (small, terminal fins; rounded posterior end, etc.).

9. The anatomical characteristics of Oegopsida are in general deviations from the type of Decapoda. This applies particularly to the following characteristics: a) the embryos of Oegopsida show the same state of "anlage" as the Myopsida (Naef, 1910, p. 320); one venous branch disappears later and is replaced with an anastomosis, hence the deviation; b) the origin of the genital artery in the heart is typical for all Cephalopoda (cf. Naef, 1913); it is present in Nautilus and in the Octopoda. The heart of the Oegopsida has a different structure (during development), in which an anastomosis forms an indirect connection to the genital artery.

These facts contradict the arguments for the systematic unification of the Loliginidae with the Sepioidea and their separation from the Oegopsida.

The formation of the primary eyelid of the Oegopsida retains the primary pattern of all Dibranchiata (Decapoda). The "Myopsida," on the other hand, show a rather uniform deviation from this type. In other respects, however, the Oegopsida deviate strikingly and secondarily from the common ancestral form. Some special characteristics are in contrast to the typical conditions, which persist in the "Myopsida." Characters characteristic for a wider group cannot be used logically for the definition of a smaller group. A systematic arrangement in a genealogical tree can only be based on characters which represent monotypic metamorphoses of the primary constitution. It appears from the above that it is dangerous to use a single character for the definition of a group (like the cornea of the "Myopsida"). If the systematist were forced to do so, he would have to determine whether the resemblance in this particular character is at least monotypic, i. e. whether it is present throughout the morphogenetic process.

c. TYPICAL STRUCTURE OF THE ADULT ANIMAL

Our concept of the ancestral form of all recent Metateuthoidea* closely resembles Prototeuthis (Figure 53 on p. 136). The important difference is the form of the gladius as derived on p. 144 (Figure 62 on p. 146), which has an anteriorly narrowed, free rhachis and posteriorly a leaf-shaped flag which consists of lateral plates and cone flag and passes terminally into a spoon-shaped form or a cone. The asymptotes which delimit the lateral plates and cone flag (p. 146) also indicate the morphological separation
156 from the proostracum and conotheca. The cone is covered with the remnants of a stratified sheath. We must therefore also assume here the presence of a true rostrum which is comparable to that of the Belemnoidea. The Prototeuthoidea still show definite traces of such a structure, e. g. in fossil shells of Plesioteuthis, although the posterior end is usually destroyed. In the Mesoteuthoidea, I found no trace of it, and the entire form

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* Fossil gladii of this group may possibly be found in Cretaceous or Tertiary strata (slates). (See, however, "Fossile Tintenfische," 1922, p. 154, and p. 162 below.)

of the occasionally well preserved, markedly rounded cone makes the existence of a distinct terminal spine most improbable. However, a small remnant in form of a knob or short spine may have been present also in the shell of Palaeololigo (Figure 62 on p. 146; compare Lycoteuthis, Figure 125, or Sepia, where the rostra are sometimes preserved, sometimes reduced, as in S. elegans). Such a remnant may well have disappeared during fossilization. The posterior end of the shell of Mesotheudoidea is usually damaged, and the absence of the rostrum in these predecessors of the Metateuthoidea proves little because both the Loliginidae (Chapter 6) and the Oegopsida (Chapter 9) have a strikingly similar rudimentary structure: a laterally compressed, pointed structure situated dorsally on the posterior end and marked with lines radiating from the apex of the cone (pp. 150 and 171).

A new element appears here in the relationship between animal and shell. We rejected earlier (p. 92) the view that in the Dibranchiata the mantle grows around the shell. Something similar, however, takes place subsequently in the Metateuthoidea, in which the attachment of the muscular mantle becomes removed from its primary position at the shell margin (cf. its development, Figure 25, p. 94) and advances on the outer surface of the shell. A similar process takes place in the Sepioidea, but in a very different manner. The gladius, which in the Metateuthoidea is elastic and not calcified, in contrast to the fossil predecessors, is drawn thus into the sac of the muscular mantle. It helps in swimming to expand the mantle mechanically between the rhythmic contractions, like the gelatinous umbrella of the medusa. The gladius, the dark outline of which is usually visible through the skin of preserved, slightly macerated, small specimens (Figure 67 on p. 161), is therefore not completely visible, but narrower by the stripe on which the muscles originate. The gladius is attached to the free shell margin only at the posterior end, so that the cone is completely visible in ventral view (Plate IV, Figure 1).

The fins are markedly larger than in Prototeuthis and form together a transverse rhomboidal or heart-shaped figure (Figure 65 on p. 153). Their attachment extends to the posterior end, where a skin fold (Fh) provides a connection with the apex of the body which is supported by the rostrum. The fins are thus posteriorly contiguous and fused with the apex of the body. The areas of attachment diverge anteriorly at an angle, leaving
157 a considerable part of the translucent flag of the gladius ("lanceola") between them free. Their articulation with the shell permits movements in the median, lateral and anterior direction, as far as the elastic attachment at the posterior end permits. Special skin muscles serve for this purpose.

The mantle margin, neck folds, olfactory organ, funnel pits and eye region resemble those of Prototeuthis (p. 139). The arm apparatus of Prototeuthis may also be considered as typical for the Metateuthoidea. The correction of our previous concept (p. 147) must be considered here: Hooks are a special character of some Oegopsida among the Metateuthoidea and not a general characteristic of the Teuthoidea which would have to be considered as a typical resemblance between them and the Belemnoidea. What has been stated above (pp. 127—133) for Metadecapus is true only

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* The opposite occurs in the Prototeuthoidea, in that the mantle musculature projects onto the inner side of the lateral plates; this is clearly visible in many specimens (Foss. Tintenf., p.114).

158 for the later Belemnoidea (Naef, 1922, Fossile Tintenfische, particularly Figures 62 and 91). Neither the Teuthoidea nor the Sepioidea have hooks; both developed from an early form of Belemnoidea (Aulacoceratidae; see p. 135) which had only suckers and which was described as Protodecapus (p. 109—127) in general outline. No Proto- or Mesoteuthoidea had hooks; the statements of Münster, Meyer, Wagner, Walther (p. 147) on this are erroneous. (Cf. also Zittel, 1885, Figure 713 on p. 519, which can be misleading; see also my book on the fossil Cephalopoda, loc. cit.)

(157)

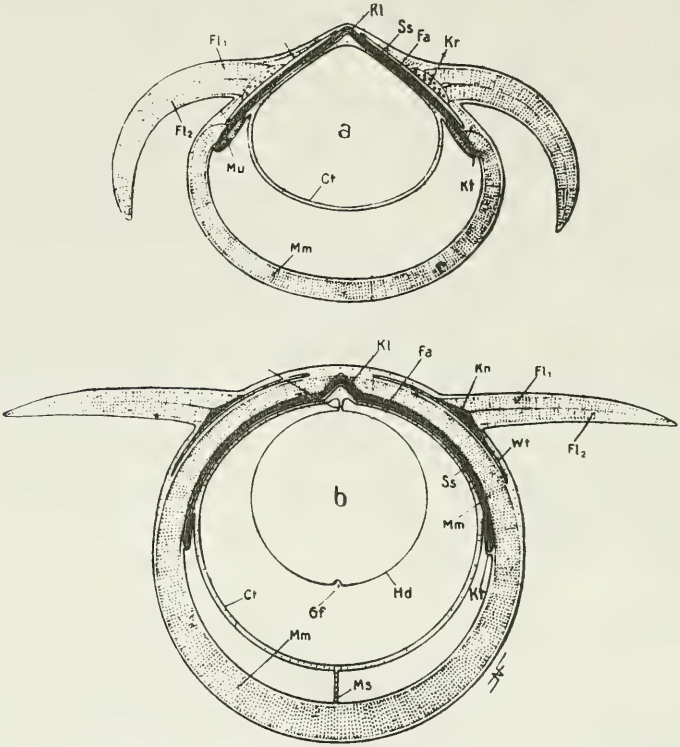


FIGURE 66. a) Cross section through the posterior part of the body of a young Pterygioteuthis in the middle of the fins (diagrammatic, after Tippmar, 1913, p. 518, with interpretations). Note the pocket of articulation of the fins (without letter); the keel of the rhachis (Kl); the fin cartilage (Kr); the insertion of the muscular mantle on the outer side of the shell margin; the attachment of the funnel and the cephalopodial retractors (Mu) on the inner side of the shell margin, which is directed otherwise free toward the mantle cavity and is covered by the remnants of the primary mantle; the shell margin (Kt) which projects into the mantle cavity.
b) Corresponding section through an older, higher form of Metateuthoidea. The gladius is surrounded by the muscular mantle to such an extent that only the keel is free under the dorsal skin. Lettering as in Figure 56 on p. 139. The muscular mantle has grown upward on the outer side of the shell in section b, forcing the base of the fin away from the shell sac and to the outer side of the muscular mantle; the base of the fin remains, however, unchanged in principle. See p. 163.

The tentacles require particular consideration. In the recent Metateuthoidea and in their fossil relatives (p. 143) they are specialized as described for Protodecapus (p. 117—120) and in this respect resemble the tentacles of the Sepioidea. However, the tentacles of the later Belemnoidea (loc. cit.) closely resemble the other arms. A characteristic of the stalk of the tentacle is a narrow outer longitudinal skin fold, the "stalk margin". This fold reaches to near the beginning of the swimming margin of the club but ends slightly ventral to it (cf. Loligo, Ommatostrephes). The "stalk margin" is indistinct in some Metateuthoidea.

The stalk of the tentacle is long and bears a zigzag row of very small suckers which become more numerous at the transition to the hand part and thus suggest a special "carpal part" (cf. Oegopsida, Chapter 9). The suckers form a transition from the biserial to the quadriserial and octoserial arrangement.

The arrangement of the suckers is asymmetrical in these two proximal parts. A sucker on one tentacle usually corresponds to an interval on the other. When accelerating forward, the Teuthoidea usually keep their tentacles close together and the suckers of the stalk and carpal region hold the tentacles together. The other arms are then ready to capture the prey (cf. p. 228).

The suckers of the hand part are arranged in 4—8 rows, those of the median rows are enlarged but never modified into hooks, so that both the median and the marginal rows bear normally toothed horny rings. The hand part passes gradually into the narrow distal part in which the suckers are normal, quadriserial and rapidly decrease in size. The last 2 or 3 suckers of the 4 rows form a terminal part on which the suckers are slightly larger, flat, and firmly attached to the base which is a solid, muscular plate, slightly curved inward and upward at rest and in preserved specimens.

The swimming margins also show some special characters. To understand these structures it has to be remembered that the Teuthoidea show a tendency of adaptation to nektonic life and that their arms serve as rudders in swimming. In accordance with this tendency, the swimming margins of the lateroventral arms are here particularly large; during postembryonic development, they gradually grow to the base of the arm and become very
159 wide, especially in the middle of the arm, so that they become strong, muscular rudder surfaces (compare, for example, Sthenoteuthis). The swimming margins of the dorsal arms are more delicate and also often extend to the base of the arm. The margins of the laterodorsal arms become smaller postembryonically and are replaced functionally, at least in the proximal part of the arm, by the lateral outer edge of the arm, which develops into margins and is connected with the true swimming margins. These parts also contribute to the rudder action of the arms, although their effect is rather small compared with the powerful, laterally angular margins of the lateroventral arms (Figure 238).

The mouth region is also of particular interest. The 6 typical buccal pockets of the Decapoda (p. 122) are here particularly deep and large, so that not only the distal but also the proximal part of the buccal mass ("buccal cone") is exposed (Figure 45 on p. 119). The buccal mass becomes therefore more mobile, as at the bases of the muscular arms, by the invagination of the tentacle pockets (p. 121). Because of the invagination, the buccal pockets become the bases of the buccal pillars (or "buccal arms") and are pressed outward toward the outer arms, while the bases of the connecting membranes are pushed toward the mouth cone, so that these two structures can be moved far apart from each other. The only remaining connection between the buccal pillars and the basal part of the buccal membrane is by skin folds which remain stretched between two adjacent buccal pockets. These folds are very delicate and may tear in many Metateuthoidea, creating deep circumoral slits which connect the buccal pockets. Since there is no true deep pocket between the ventral buccal pillars and the adjacent lateral pockets are contiguous in the middle, dorsal to the pillars, only one septum which divides the two pockets corresponds to the two pillars (Figure 79) and is connected with the base of the buccal membrane on the buccal cone which is thus hexagonal. The buccal funnel becomes therefore divided into 6 parts, a preliminary stage to the condition in the Octopodoteuthidae and Histioteuthis (see below; Plate III, Figure 2). A fusion of the two ventral buccal pillars may easily take place as their bases are situated close to the origin of the median septum which connects them.

Characteristic but typical characters of the Metateuthoidea are the windows on the eye chamber on the upper and lower side of the head (Plate IV). Light that may perhaps pass through these windows is reflected on the inner side of the eye chamber and reaches the lens indirectly. However, the windows suggest more probably luminous organs (perhaps rudimentary) which exist on corresponding parts of the bulbus in most Oegopsida and could be assumed to have been present already in Metateuthis, perhaps in diffuse form. Such windows, however, are also present in the Loliginidae and other types in which luminous organs have not yet been found near the
160 eyes, at least on the ventral side of the head (Figure 97 on p. 210). They are well defined, transparent, thin areas of the wall of the head on which iridocytes and chromatophores are scarce or absent. The light passing in either direction through the windows meets no obstacle, dispersion or reflection, and this certainly needs an explanation.

A detailed characterization of the group on the basis of anatomical characters would be possible, but this cannot be done at this point. The above data should be sufficient to establish the close relationship between the Loliginidae and Oegopsida.

d. TYPICAL POSTEMBRYONIC DEVELOPMENT

For general orientation about the development, consult first the preceding chapter (p. 141), especially with regard to the displacements resulting from the simplification of the chambered shell.

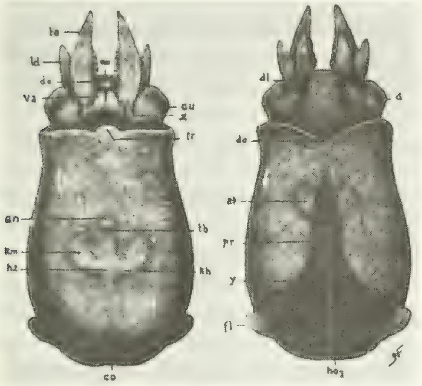
One would expect that the above derivation of the form of the gladius of the true Metateuthoidea would be evident in their embryogenesis. This, however, is the case only to a restricted extent, as the ontogenesis of our forms no longer passes through an actual belemnoid or prototeuthoid stage. However, these early stages are clearly reflected in the following characters:

1. The cone of young animals is always stronger than in the adults, regardless of to which degree it is preserved later. Its proportions, however, vary greatly in freshly hatched or even embryonal stages. We naturally regard as typical (p. 19) those with a most highly developed cone (Figure 67). Such a cone is scooplike, rounded, covered only by the shell fold and bears on the outside the small, rounded, subterminal fins in the typical position.

It is not surprising that its form is not pointed conical. Belemnoidea must first build the rounded embryonic chamber (Figure 36 on p. 107) before conical growth can begin. This is in fact an example of the general embryonic type of Decapoda (Dibranchiata). The muscular mantle is attached around the shell margin, from which it contrasts sharply by its light coloration in preserved embryos.

2. The proostracum is as should be expected in a Beloteuthis (Figure 62 on p.146): it is narrow anteriorly and tapers to a sharp anterior point, so that the stellate ganglia are situated close together. It should be mentioned, however, that in the younger (embryonic) stages (cf. Vol. II, Plate VIII, Figure 10 and Plate IX, Figures 10 and 12) the part corresponding to the proostracum is wider and reminiscent at least of the Prototeuthoidea.

(161)



161

FIGURE 67. Freshly hatched juvenile stage of a species (X) of Oegopsida (perhaps Calliteuthis or Thysanoteuthis). This animal, which developed from a pelagic batch of eggs, could not be identified with certainty (see Vol.II, Plate VIII), but it is a typical larva of Oegopsida with partly still embryonic characters. For example, the primary lid fold is not yet developed (points "d" and "x" should be connected laterally by a thin fold behind the eye). A striking character is the large, scoop-like cone (co) which surrounds the posterior end as a dark, translucent membrance and bears small, lateral, posterior fins (fl). Anteriorly and dorsally, the cone passes into a narrow proostracum (pr), next to which the stellate ganglia shine through (st):

ho_2 – lateral arm of Hoyle's organ; y – attachment of muscular mantle on the gladius; hz – heart; km – gills; an – anus; tb – ink sac; kh – branchial heart (organs shining through the mantle); tr – funnel; au – eye; va – ventral arm; do – outer yolk sac (rudiment); ld – laterodorsal arm; te – tentacle; mu – mouth; dl – gland ridge (cf. Figures 307 and 346). 20×.

A more detailed comparison between the different parts of the juvenile shell with that of the adult would be desirable (cf. Figure 62 on p. 146). A large part of the dorsal part of the spoon apparently corresponds to the lateral plates. To indicate the delimiting lateral and median asymptotes on the left, it would be necessary to draw lines from the posterior end of the figure to the point "y" on the shell margin and the stellate ganglion. However, these parts are not very distinct in the juvenile stage, and the primary form of the shell is here still undifferentiated. The morphology of the shell of the Dibranchiata and the relationship of the shell to the soft body can be studied in detail during the very instructive transitional stage before us.

The further development of the Metateuthoidea shows special characters only on the posterior part of the body. The typical changes can be understood by comparison of Figures 65 and 66 on pp. 153 and 157. These changes culminate in a slow displacement of the correlative proportions of gladius, muscular mantle and fins. On the gladius, the cone lags behind in growth and becomes relatively smaller, but sheath and rostrum develop on the outer side of the gladius. Cone flag and lateral plates grow into the flag, and the rhachis becomes longer. The muscular mantle assumes its definitive attachment on the outer side of the margin of the flag (p. 153). The fins grow, and their attachment extends

anteriorly, posteriorly and in the middle. By their displacement posteriorly, the fins assume their natural position at the end of the body, the connection being made by a more or less membranous area (Figure 65, Fh) the elasticity of which permits some movement of the articulation despite the fixed position at the posterior end. Following the development of the flag, the fin advances slowly anteriorly, forming the typical "ear lobe," at first without losing the primary contact with the shell (p. 113). The fins become con-
162 nected in the middle, at first at a single point near the posterior end, but without becoming fused; they form blunt lateral angles which finally result in the characteristic rhomboidal- heart-shaped outline shown in Figure 65.

e. VARIATION OF THE TYPE OF METATEUTHOIDEA

We explained above in detail (pp. 144–146) that the Metateuthoidea are the recent descendants of the fossil Proto- and Mesoteuthoidea and that there is no sharp boundary between them and the latter two groups. The gladius of Beloteuthis resembles a stalkless leaf. Next appeared forms in which the anterior margin is produced into a point and finally into a long free "rhachis" resembling the stalk of a leaf (Figure 62 on p. 146). It may be assumed from the latter condition that they belong to the Metateuthoidea, although they still resemble Beloteuthis in details like the growth lines and the wide form, and there are, in fact, transitional forms between these forms and Beloteuthis. However, Palaeololigo cannot be placed in the recent groups of Metateuthoidea, and one must therefore draw a boundary of steps between the fossil and recent Teuthoidea. It is evident from the names Proto-, Meso- and Metateuthoidea that they are merely successive stages of a metamorphosis (Introduction, p. 17).

Let us now consider the variation of the Metateuthis type in the recent species. We have first to determine the general principles that apparently govern the variation within the group, which is best done by examination of the general ontogenetics of the Metateuthoidea. This will provide a better understanding of the variety of forms in the group as a whole and in its main groups Metateuthoidea, Oegopsida and Myopsida, which are closely related and this is also reflected in the variation of the common type.

The best method of expressing these relations would be the reconstruction of an even more specialized common ideal or ancestral form. However, this does not seem to be the correct approach, because a uniform tendency of variation is more likely to create a number of common secondary characters than a fixed ancestral form and we have mainly to follow the morphological and ecological consequences of the evolution of Metateuthis. These tendencies are mainly towards simplification which is expressed in the shell in a progressive reduction of the cone, the growth of which ceases at an ever earlier time until it is only still distinct in the embryonic and early larval stages (Figure 87 on p. 187); injuries and deformations of the delicate posterior end obscure the existence of the cone in later life. This is usually accompanied by a reduction of the rostrum. The rearrangement of the suckers from a biserial to a quadriserial arrangement on the arms, and from quadriserial to octoserial on the club

163 of the tentacles is suppressed in most species. The mouth arms usually bear no suckers, or the number and structure of the suckers is reduced (cf. particularly the Enoploteuthidae).

These changes can be interpreted ontogenetically as phenomena of inhibition associated with an adaptive specialization by simplification. Other phenomena may be considered as progressive. As should be expected of progressive changes in general, they are connected with the typical early stages and are distinct in the course of ontogenesis.

As has often been observed in adult Prototeuthoidea (Figure 60 on p. 143), the fins of young Metateuthoidea (Plates I and V) occupy only a small part of the mantle and are at first subterminal (Figure 67), i. e. they do not yet reach the posterior end (apex of cone) of the mantle sac. This takes place during the postembryonic development, when they attain their characteristic pointed form (Figure 65). The posterior extension of the base of the fins results in their fixation since the fin reaches a natural boundary and also achieves a mechanical attachment. The posterior end of each fin becomes fused with the tissue enclosing the cone. This creates an apparatus for cutting through the water, which is important for the strong swimmers of the group.

Due to the elasticity of the fins and their articulation with the shell sac (Figure 66 on p. 157), the anterior margin of the fins remains movable, and the length of the fins is physiologically variable, which the systematist should not overlook. The progressive lengthening of the fins in the anterior direction is easy to understand. It takes place during the postembryonic development of many Metateuthoidea until it reaches the most anterior limit, i. e. the anterior margin of the mantle (cf. Ctenopteryx, Chapter 11, and Thysanoteuthis, Chapter 37). Naturally, this also necessarily changes the base on which the fins are situated. The cone flag already ends in the posterior part of the mantle sac. It may advance more by a median displacement to the adjacent parts of the flag, but it must pass soon on to the muscular mantle: as the articulation of the base of the fins (Figure 56 on p. 139) is no longer directly connected with the shell sac, it may project above this, which would not have been possible in the original type (Figure 26 on p. 95). The fin then glides in the anterior part of the muscular mantle and posteriorly on the shell. Another displacement seems even more important, which we assumed to have begun already in the ancestral form and which developed during the postembryonic development of Metateuthoidea. The primary point of origin of the muscular mantle is the margin of the mantle from which it does not move far in juvenile forms, even if it occupies part of its outer side, at least anteriorly (Figure 66a).
164 However, at a later stage the gladius becomes increasingly enveloped by the muscular mantle. In some forms (Loligo), this envelopment becomes almost complete (Figure 71 on p. 170). This has no connection with the primary enclosure of the shell, which begins from the shell fold and not from the muscular mantle (p. 51).

As a result of the secondary change described, the gladius moves more and more into the interior of the tube of the muscular mantle. The pocket of articulation of the base of the fin is thus pushed gradually away from the shell sac also in the posterior part of the body, because the muscular mantle enters between them. The connection between fin and shell may be replaced finally in the whole area by a connection between fin and muscular mantle.

The typical relationships are expressed here but the change takes place only in the postembryonic stage. The final degree of modification differs considerably. In some types (Loligo, Figure 71) the rhachis is also completely enclosed, so that the gladius of the adult is situated entirely in the mantle tube. In most species, however (Onychoteuthis, for example), at least the median keel is visible on the surface or becomes visible after removal of the skin. In other cases, also the part of the flag situated anterior and medial to the fin base, i. e. the part which forms the pointed anterior projection, remains free. This part was named lanceola (Pfeffer, 1912); it is distinct in macerated, bleached or skinned specimens, as well as in translucent young forms, e. g. in many figures of very young Oegopsida, in which the lanceola is at least a transitional stage (cf. also Plates V, VII, VIII in Vol. II).

This displacement of the origin of the muscular mantle is certainly a further step in the direction originally taken by the Teuthoidea (p. 137) as it is associated with a further growth of the musculature at the expense of the supporting skeleton. The gladius of Prototeuthis still occupies at least the dorsal quarter of the mantle sac (Figure 56 on p. 139), converting the groovelike, dorsally open muscular mantle into a tube or sac and giving it its solidity. In the later forms the stability of this part of the body depends more and more on the mantle itself, the thickness of which increases considerably. This development advances even further, as we shall see in the Oegopsida (Ommatostrephidae, for example). In Figures 70—71 on p. 170 the flag still supports distinctly the muscular mantle on its outside and contributes mechanically to its expansion by its elasticity (p. 93). In the above forms, on the other hand, the reduction becomes progressively more marked until the muscular mantle becomes quite independent in the statics of its form and in the dynamics of the swimming and breathing movements which result in a further strengthening of the muscular tissue (Chapter 32). Another morphological tendency is connected with the widening of the tentacle pockets. These not only cause the tentacle stalks and the muscular bases of the ventral and lateroventral arms to project from the head, but they also tend to extend toward the dorsal side of the head on the median side of the
165 eye, between the arm mass and the wall of the eye chamber (cf. Chapter 6, Figure 76 on p. 177). This tendency is stronger in the Loliginidae than in most Oegopsida, although the large tentacle pockets cannot accommodate the coiled tentacle stalks (such a condition is, however, present in the otherwise very similar Benthoteuthidae, particularly in Ctenopteryx (q. v.; Chapter 40).

Although these tendencies are relatively similar in the Metateuthoidea, they can be divided into two typically different groups of forms the position of which cannot be clarified at this point because several rare types of problematical position (Promachoteuthis, Lepidoteuthis) would have to be studied. It can be decided, only when this has been done, whether the two categories are coordinated or whether they are a central group and a derived group. (This is the old problem, mentioned on p. 150, of whether the Oegopsida or the Myopsida are more "primitive.")

One of these groups is identical with the Oegopsida d'Orbigny and should retain this name if the revised systematics should not produce more confusion than order. The other group corresponds to the "Myopsida" but without the Sepioidea. I shall retain also the name Myopsida but in a slightly modified form. The groups defined are, therefore, the Metateuthoidea myopsida and the Metateuthoidea oegopsida, although the opposition proposed by d'Orbigny (p. 149) is restricted here to one subgroup and not applied to the Decapoda as a whole. I had proposed this solution already in 1916, as I was then dealing with only the recent forms and not yet with the Proto-, Meso- and Metateuthoidea.

APPENDIX*

METATEUTHOIDEA MYOPSIDA

(d'Orbigny, 1845) Naef, 1921

DIAGNOSIS

Primary lid closed above the eye, so that the orbit is closed except for a narrow pore at the point of the sinus and forms a tough, transparent cornea above the eye. Female with typically developed accessory nidamental glands. Embryo with an external yolk sac. Development of arms
166 more or less simultaneous; development of ventral and lateroventral arms not lagging markedly behind that of the other arms in early youth. Suckers biserial on the arms, quadriserial on the tentacle clubs. Suckers not transformed into hooks.

For a distinction from the Sepioidea with rudimentary shell, which may also assume the form of a "gladius" (Sepiolidae) or be absent, so that the habitus is Loligo-like (Idiosepius), the following characteristics are added: a strong adductor pallii medianus is absent. Tentacles not, or only slightly, retracted in the tentacle pockets. Gladius well developed and extending to the posterior end, at least in youth, later occupying the greater part of the dorsum.

COMPOSITION OF THE GROUP

This group includes first of all the Loliginidae, including the isolated and only incompletely known genera Promachoteuthis Hoyle and Lepidoteuthis Joubin, which apparently belong to the Loliginidae. The position of Promachoteuthis in this group is evident from the formation of a true cornea with an ophthalmic pore (see the original figures in Hoyle, 1886, Plate 14, Figure 10), for Lepidoteuthis this follows from the structure of the heart (Naef, 1912, p. 243). Lepidoteuthis does not belong to the Oegopsida in any case because the arrangement of the arteries from the heart differs from that in Oegopsida, in which the genital artery originates from the posterior aorta. Lepidoteuthis certainly belongs to the Teuthoidea and, in its general habitus, resembles Alloteuthis subulata.

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* Because of the brevity of this part and its close connection with the above text, and due to the incomplete objective classification, I do not give it as a separate chapter.

Hoyle determined Promachoteuthis as belonging to the Sepiolidae. However, as a specialist of this family, I object to this. If Hoyle's drawings are only in part exact, Promachoteuthis can only belong to the Teuthoidea; it is certainly a markedly aberrant form among the recent Decapoda. Further study of the original material is necessary. Unfortunately, the tentacle clubs of both genera are unknown; the same applies to the eyes and the other arms of Lepidoteuthis.

TYPICAL CHARACTER OF THE GROUP

What was stated on pp. 150—152 also applies to this group, and the Metateuthoidea myopsida include all recent Metateuthoidea which do not differ from the general type like the Oegopsida. However, the group has special characteristics which apply to all its members as far as can be judged on the basis of our present knowledge.*

167 The formation of the cornea is characteristic for the Metateuthoidea myopsida. The cornea develops as follows during the later part of the embryonic development in the Loliginidae. The primary lid closes over the eye, leaving only a small pore (Plate I, Figure 2; cf. Vol. II, Plate VI). The pore persists at the point of the sinus, which we assumed to be present also in Prototeuthis (Figure 51 on p. 136) and which is present in most Oegopsida. It provides a permanent connection between the eye chamber and the surrounding medium. The raised, strongly convex part of the primary lid which covers the eye (Figure 68) is the cornea. It becomes a tough, smooth, transparent skin (without chromatophores or iridocytes) which protects the eye without impairing its function. The cornea of live specimens is not hard and horny, but soft and pliable and keeps its form due to the tension in the eye chamber. As the inner part of the orbital pore has a kind of ball valve, the escape of fluid is prevented.

The arrangement of suckers is biserial on the arms and invariably quadriserial on the hand and distal part of the tentacle club. A change of suckers into hooks has never been observed, nor does it begin in any way. Dentition of the "horny rings" is general.

In other aspects, the habitus of the ancestral form is as in Metateuthis (Figure 51 on p. 136 and Figure 63 on p. 150).

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* This group can, therefore, not be considered as the central group of the Metateuthoidea.

FAMILY LOLIGINIDAE
s. restr. Steenstrup, 1861*

Contents: a. Diagnosis. — b. Typical structure of the adult animal. — c. Typical postembryonic development (p. 187). — d. Variation of the type of Loliginidae (p. 191).

a. DIAGNOSIS

Gladius typically feather-shaped, pointed anteriorly and with a median keel, with a very rudimentary, spoon-shaped cone at the posterior end which is usually present only in young forms. Muscular mantle completely surrounding the gladius, so that only the edge of the keel is still visible through the skin. Fins contiguous posteriorly in a thin ridge. Suckers biserial on the arms, quadriserial on the tentacle clubs. Pockets of gill roots opening posteriorly in the mantle cavity (i. e. they are open). Dorsal pair of arms less developed than the others. Strictly nektonic animals, always living near the coast or the bottom (not in the open or deep sea).

b. TYPICAL STRUCTURE OF THE ADULT ANIMAL

We begin here to deal with smaller categories (p. 12), and the description of ideal morphological types will be gradually replaced by that of real forms. However, also descriptions of species should not give only isolated observed facts. This could be done only by the description of an individual animal
169 or preparation. The descriptions of species on the other hand, deal with typical structures, morphological norms and ideal forms. Types and variations exist within the species as well. This should be considered as a principle, even if we have to admit that direct observation and morphological abstraction are practically inseparable, at least at the level of accuracy which we attempt or are able to reach. In the description of the different

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* About the gradual restriction of the composition of the family see Jatta (1896, p. 165). In d'Orbigny (1826), the family still includes all the known recent Teuthoidea; Owen (1830) places here even the Sepiolidae (as "Teuthidae"). Férussac and d'Orbigny (1836) defined the family roughly like the Teuthoidea in this work (p. 47), including also the fossil Leptoteuthis, Beloteuthis and "Teudopsis." Gray (1849) again included the Sepiolidae, but d'Orbigny (1845, 1855) removed them from this family. In Keferstein (1866), the only foreign body in the family is the genus Palaeololigo (Teuthopsis), not without some justification (see p. 156); Keferstein places the family in the "Chondrophora" under a) "Myopsidae," next to the Sepiolidae. Woodward (1871) published a similar classification. Tryon (1879) again includes the fossil Teuthoidea in the Loliginidae. The family appears in its recent definition in Steenstrup (1861) under the name of "Loliginei." We hope that the present volume gives them their definitive position.

species we will occasionally mention variations from the norm. The discussion, however, will consider the norm — as far as we consider it as existing. If circumstances permit, we shall select the typical individuals from abundant material and disregard aberrant details (p. 43). In other cases, the rarity of the specimens makes it necessary to describe the available structures. The principles of the morphological primacy obviously apply also to the species, and the determination of the norm does not coincide with the average (cf. p. 18). On the other hand, a single representative (individual, species or genus) may be considered as typical within a species, genus or family.

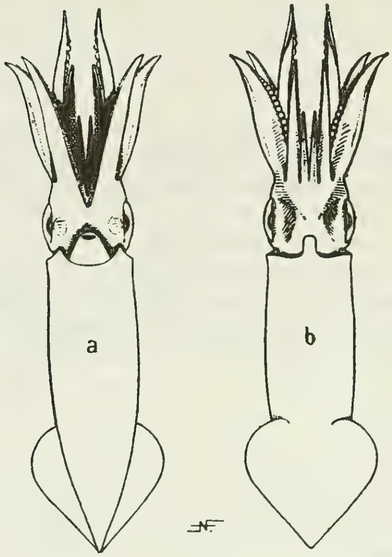

FIGURE 68. Young female of Alloteuthis media, natural size. The figure shows at least the typical habitus of live Loliginidae. However, the dorsal margin of the mantle already shows the special character of the genus; in the ancestral form this structure may be assumed to be projecting in a very blunt median angle, as in Sepioteuthis (cf. Figure 64 on p. 152).

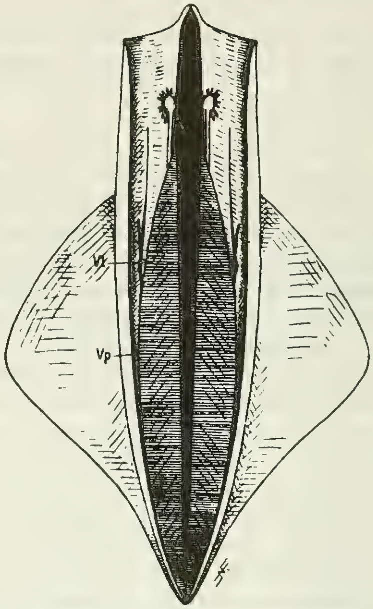

FIGURE 69. Situs of mantle and shell of Loligo vulgaris, half natural size. Compare with Figure 34 on p. 104 and Figure 58 on p. 141, which show the same relationships, as well as Figures 84, 85 on p. 185 and Figure 92 on p. 200, which are drawings of the same specimen before preparation. Note: gladius, muscular mantle, fins, gill bands (attachment on the mantle), stellate ganglia, and fin nerves. The posterior boundary of the dorsal mantle cavity is visible as a curved line between the stellate ganglia. The part of the gladius anterior to this point bears the collar bond; in the living animal, it is situated opposite the neck bond:

Vl — lateral pallial vein; Vp — posterior pallial vein (or its exit from the muscular mantle).

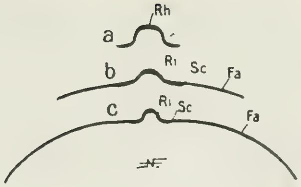

FIGURE 70. Cross sections through the gladius of Loligo vulgaris:

a — in the free anterior part of the rhachis; b — through the anterior part of the flag at about half ist width; c — at the widest part of the flag. Note the curvature of the rhachis (Rh) and its thickening opposite the flag (Fa) with the formation of thin longitudinal ribs (Ri). Sc — lateral margin of rhachis. Natural size.

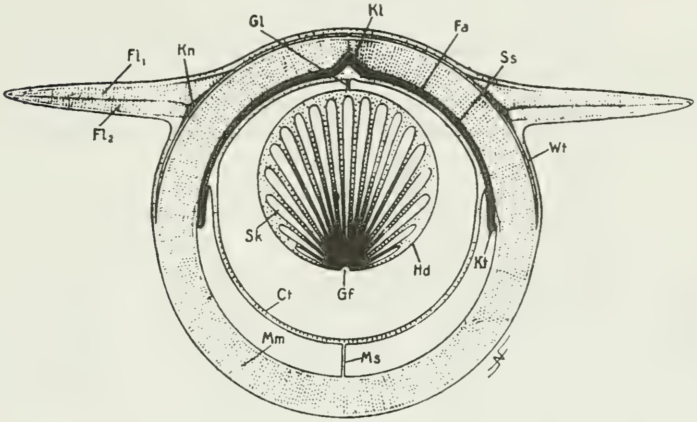

FIGURE 71. Topographic relationships between gladius, muscular mantle, fins and mantle cavity in typical Loliginidae. Diagrammatic cross section through the posterior part of the body in the widest part of the gladius. The muscular mantle has completely surrounded the gladius (p. 164) above the rhachis (compare with Figure 66 on p. 157), so that the fins and their articulation pockets are situated entirely on the muscular mantle. The gladius is situated on the inner side of the mantle during preparation, as shown in Figure 69 on p. 169:

Fl_1, Fl_2 — upper and lower muscle layers of fin; Kn — fin cartilage; Gl — genital ligament; Kl — keel of rhachis; Fa — flag part of gladius; Ss — shell sac; Wt — articulation pocket of fin; Kt — lateral edge of gladius projecting toward the mantle cavity; Hd — testis; Sk — sperm tubules; Gf — their opening groove; Ct — coelothelium; Ms — mantle septum; Mm — muscular mantle.

Not a single recent genus or species of this family answers these requirements even in part, i. e. no recent form combines all primary characters. We must therefore construct another ideal or hypothetical ancestral form "Protololigo," from which the recent species can be derived.

For the establishment of this ancestral form we can use descriptions of actual species and preparations for nearly all parts, selecting only those which show the typical relationships at least in part. We anticipate in this a large part of the special descriptions, and will give only the particular characteristics in the descriptions of the various genera and species.

171 The general habitus closely resembles that of the young Alloteuthis shown in Figure 68 on p. 169. It has, however, some specific characters which will be described below. At any rate, it is a rather slender animal which swims or floats well and never rests on the bottom. All Loliginidae are strictly nektonic, although they live close to the bottom and shore and never move far from the surface or the shore. We assume that the ancestral form has the size of an average Loligo vulgaris which it may also resemble in coloration.

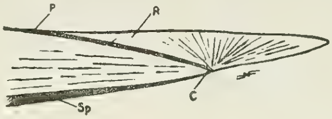

FIGURE 72. Lateral view of the transparent posterior part of the shell of Alloteuthis media (20×). Optical section showing the small but distinct cone and the rudimentary rostrum situated dorsally on the cone. The rostrum resembles strikingly that of the Oegopsida (Onychoteuthidae and Gonatidae; cf. Figure 63 on p. 150). An example are the lines which radiate like a fan from the posterior end of the cone and indicate the direction of growth:

P – proostracum, i.e. rhachis of gladius in optical section; C – cone, same; Sp – slit between diverging margins of flag; R – rostrum.

The relationships between mantle and shell are shown mainly in Figure 69 on p. 169, which is an empty preparation of the situs of Loligo vulgaris. The gladius is situated entirely inside the mantle tube and has the general form that is characteristic for the Metateuthoidea. The gladius is covered anteriorly by the collar bond, i. e. the part of the primary mantle which is slightly cartilaginous and is situated opposite the neck cartilage. The mantle cavity extends posteriorly between the stellate ganglia, which are situated close together, as we had to assume already for Metateuthis (Figure 64 on p. 152). The anterior end of the gladius (Figure 62 on p. 146) is pointed, but the apex is very thin and delicate and often broken in preparations, which explains the inaccuracy of most illustrations. The thickened, longitudinally striped, groovelike rhachis can be recognized which is almost the only part present before the stellate ganglia (cf. Figure 69). The rhachis is connected further on, on each side with the leaf-shaped flag, in which it extends in the midline to the apex. A small, spoon-shaped cone is present at the posterior end in sections of older embryos or in very young animals. In adult Loliginidae, the cone is usually not visible because it is very small and delicate. Intact gladii of larger specimens are scarcely available, since the animals often, especially in captivity, knock against objects posteriorly and injure the delicate cone part of the shell. In the American species Loligo pealei and some other forms, however, the cone is clearly visible in adults (cf. Verrill, 1881). This part is of particular interest in Alloteuthis
172 for a morphological analysis. This genus has a distinct, if only small cone, and a well recognizable rostrum which resembles that of some Gonatidae and Onychoteuthidae (cf. Pfeffer, 1912, Plate 10, Figure 5; Plate 12, Figure 2). Like the entire gladius of the Metateuthoidea, the rostrum is not calcified,

but soft, a mere remnant incapable of supporting the characteristic end of the body of Alloteuthis. There is a striking resemblance to the homologous structure in the Onychoteuthidae. The rostrum is also laterally compressed and of characteristic structure which consists in a fanlike pattern that radiates form the apex of the cone. The rostrum is situated dorsally on the end of the gladius, forming a keel that extends anteriorly and strengthens the rhachis. We had assumed such a structure also for the common ancestors of Loliginidae and Oegopsida, particularly Metateuthis (p. 152), from which the ancestral form of Loliginidae has to be derived.

The relationship of the muscular mantle to the gladius in the Loliginidae is shown in Figure 71. The shell is completely surrounded, except at most on a small, weak area above the keel. Otherwise, the mantle forms a closed tube around the shell, which is therefore situated inside it in preparations. The metamorphosis of Metateuthis has thus reached here its full expression (p. 164).

Figure 71 shows also that the soft body does not occupy the entire inner surface of the shell, at least not in the posterior part of the mantle sac. The lateral margins of the gladius instead project free into the mantle cavity, i. e. they are covered only by the primary mantle. The outer margin projects as a thin ridge into the mantle cavity (cf. also Figure 47 on p. 124 and Figure 54 on p. 140).

The fins are rounded, heart-shaped (Figure 69) and terminal. They are connected in the middle around the posterior end by a thin median ridge which is very characteristic for the family (cf. Figure 86). During postembryonic development (Plates I, II), the fins grow anteriorly at least a third of the way along the side of the mantle; this should also be considered as a primary character of Protololigo. The anterior attachment on the mantle forms a distinct "earlobe"; the lateral margin a very blunt angle at the widest point.

The fin base and particularly the articulation pockets of Protololigo are situated entirely on the muscular mantle at an early stage and have later no direct connection with the shell (cf. Figure 71). Otherwise, the fin base shows the typical proportions.

The mantle margin shows the 3 typical corners but without the specialization characteristic for the Loligininae (p. 191).

In the neck area (Plate II, Figure 1), the characteristic ridges assumed for Prototeuthis (p. 136) are not completely developed. The anterior transverse ridge is less distinct, while the larger posterior ridge appears only as a connection between the posterior end of the first and third longitudinal ridge of Prototeuthis, which are united by them to an ω-shaped structure which resembles an ear. The olfactory organ is situated in its typical position in the angle between the third longitudinal ridge and the
173 posterior transverse ridge; it forms a flat, oval papilla (Figure 85 on p. 185). The fourth longitudinal ridge is also present, but only as a longitudinal tubercle (Hk, p. 181).

Only the above-mentioned ear-shaped structure is constant and very characteristic for the Loliginidae. The other elevations depend on the arrangement of the subcutaneous muscles and vary from one individual to another. Different specimens of the same species and age show very different formations in this area, depending on the preservation and the condition of the animal at the time. A young male of Loligo vulgaris with particularly distinct neck folds and sharp margin of the funnel pit is shown in Plate II, Figure 1 on p. 181).

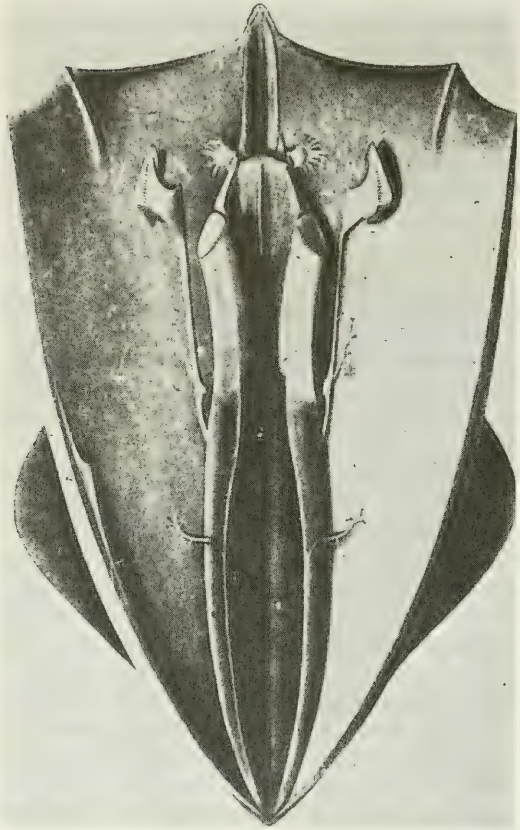

FIGURE 73. Mantle and shell situs of a young Loligo vulgaris. Natural size. The specimen is prepared like that shown in Figure 69, but spread, without removal of the ventral part of the mantle, which is only slit. The collar bond is present above the anterior end of the gladius, like the other remnants of the primary mantle (note the longitudinal ridge). The origins of the cephalopodial retractors on the shell are visible posteriorly; the anterior aorta passes in the median groove formed by the fusion of the retractors; laterally are situated the large funnel retractors, the attachment of which on the shell sac is visible. Further posteriorly, on the lateral parts of the flag, are the remnants of the primary mantle, crossed by skin folds in which the posterior vessels reach the muscular mantle. The viscera are removed. On the left side of the mantle, the rest of a median pallial septum with the median pallial artery is visible; anteriorly are situated the mantle bonds (at the margin), then the attachment of the gill ligaments, which also provide the passage of the lateral pallial veins to the body; the ends of the gills are visible.

(174)

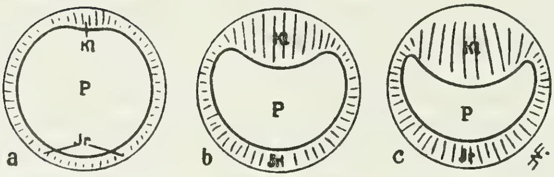

FIGURE 74. Iris fold of Liligo vulgaris in various states of contraction (diagrammatic). The normal condition is shown in c, where the lower margin of the iris (Ir) extends only slightly onto the lens, while the upper margin (Kl) overhangs the lens like a blinker. Compare the condition in the Sepiidae (Chapter 40) and Sepiolidae (Chapter 42):

P – pupil.

The eye region has a very characteristic structure. The primary lid having closed above the eyeball (Vol. II, Plate VI), leaving only a small open pore at the site of the sinus of the eye of Oegopsida (as has been presumed on p. 136 for the Prototeuthoidea and Metateuthis), the primary lid has developed into a true "cornea" which is a transparent, watchglass-shaped skin fold above the eye. It is tough, but not rigid; it is stretched by the liquid in the eye chamber.

174 The "orbital pore," the rest of the previous lid opening, is not a simple hole but a short channel which can be closed by a kind of ball valve. The convexity of this so-called "cornea," which is fixed by this valve in fresh or live specimens, is shown in Figure 68 on p. 169 and Figure 93 on p. 201. The cornea is situated free above the outer side of the bulbus, which appears more or less flattened, and also above the strongly projecting outer surface of the lens. The lens is partly covered by the adjacent iris margin and closely adheres to the opening of the iris. The dilated pupil is nearly circular. However, the iris flap (p. 96) is usually lowered and thus reduces the field of vision by preventing the incidence of light directly from above.* The area of vision can be determined by the following simple procedure. Light rays can produce pictures from all points from which the dark bottom of the eye is visible through the pupil. Observation shows that the surface of the lens of the fresh animal appears black from all directions from which it is visible (see Figure 68 on p. 169)**; this shows the importance of a pro-
175 jecting lens in the Cephalopoda (cf. Development, p. 96). At any rate, the field of vision is much greater than would be assumed from the pupil which is frequently narrowed into a crescent.†

The arms of the Loliginidae are of different length (formula: 3 = 4, 2; 1)†† The third pair is the longest, the fourth almost as long, the second much shorter, and the first the shortest. The three upper pairs are slightly "fastened" at the base by a small membrane which connects their outer edges. This connection is usually absent between the ventral arms, which may be connected briefly by the contraction of small cutaneous muscles. The connection between the third and fourth arms is developed in a manner typical for the Decapoda (p. 115), i. e. the membrane is attached to the third pair near the base but forms a wide lateral margin on the outer edge of the fourth pair and ends near the apex. The three upper pairs of arms bear swimming margins, which, however, are no longer typical for the Decapoda (Figures 110 and 136) but show the slightly modified condition characteristic for all Metateuthoidea (p. 159). Instead of being restricted to the distal part of the arm, the margins extend to its base. The details differ from one pair of arms to another. On the first pair, the swimming margin remains median and ends at the base between the lateral and median connection. The margin of the second pair is attached proximally to the outer edge, which is distinct, and it is doubtful whether it belongs morphologically to the edge of the arm (cf. p. 159). The third pair of arms has a median margin, at least in the distal and middle parts, and ends near the ventral edge (or near the presumed position of this edge), i. e. close to the attachment of the membrane connecting the third and fourth pair of arms (cf. also the chapters on the Onychoteuthoidae and Ommatostrephidae).

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* This prevents blinding by sunlight from above. In any case, such light would be of no use to the animal, since its enemies and prey live at the same or greater depth. However, aquatic birds are a danger at least for some surface-swimming species of Loligo which are often found in the open sea. The ability to dilate the pupil and the iris flap is useful.

** Figures 86, 91, 92 and others should be modified accordingly. The projecting segments of the lens, which are only protected but not optically affected by the cornea in the Loliginidae, considerably broaden the field of vision by directing rays into the pupil from below, above, behind and in front, including rays from the opposite side of the body. Each eye perceives more than half the environment, provided the iris does not restrict the field of vision, and there is binocular vision in a larger median zone situated mainly below, above, behind and in front of the animal, i.e., the ecologically important region. This is apparently a secondary improvement of the eye of Dibranchiata.

† A special stripe of the retina extends horizontally in the middle of the eye and is situated so that it corresponds more or less to the pupil (but cf. Sepia and Octopus). This is the zone of most acute and contains particularly dense rods (about 105,000 per mm^2 in Loligo vulgaris).

†† Such formulae show the relative length of the successive pairs of arms (p. 115). Their value is limited. If the arms differ only little but are very variable according to contraction or preservation, an individual measurement means nothing. I express the typical differences of length as follows: smaller ",", larger ";", equality or approximate equality "=".

(176)

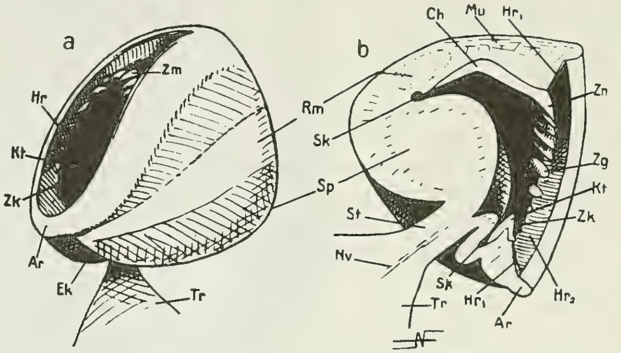


FIGURE 75. Typical suckers of the arms of Loligo vulgaris. a) Lateral view, b) section (15×). The figures show the typical condition in the Loliginidae, Teuthoidea and in the Decapoda in general, in the distinctly bilateral and slightly claw-shaped structure of the suckers (cf. Plate XII, Figure 1). The teeth (Zn) are strongly developed at the distal margin of the "horny ring" (Ch), rudimentary at the proximal margin (Zk). On the proximal part of the horny ring, however, there is a large edge (Kt) inside of the teeth which is characteristic for almost all Oegopsida. The stalk (St) is situated eccentrically on the basal pad (Tr); a musculus circularis is present, which is apparently lost in the Oegopsida (Ctenopteryx ?),(Rm).

Hr — adhesion ring; Ar — marginal ring; Ek — indentation in middle of proximal part; Nv — nerve; Sp — suction pad; Sk — suction chamber (deepest place); Mu — muscle for detachment (p. 121); Hr_1 — adhesion ring at the distal margin; Hr_2 — adhesion ring at the proximal margin.

At rest, the tentacles project by only a quarter of their length beyond the other arms, which are typically held together like a cone. The clubs occupy about one half of their length; the sucker-bearing surfaces are placed together and they extend between the other arms.

By contraction of the circular and radial musculature, the clubs and especially the stalk of the tentacle can be extended 2–4 times their length. Exact measurements, however, are not possible, and the length of the tentacles in preserved specimens cannot be used for systematic purposes.

176 The tentacle stalk is slightly compressed dorsoventrally and bears 3 more or less distinct longitudinal ridges. Two approximated ridges delimit the narrow inner surface of the arm part. They end near the base but widen toward the club, and pass into the protective margin (Figure 92

on p. 200). The more distinct outer edge of the tentacle stalk is accompanied by a very narrow "stalk margin" which reaches to the proximal part of the tentacle club, where it ends without (p. 159) passing into the swimming margin of the club, which begins slightly dorsally near the end. The swimming margin occupies the greater part of the club; it is narrow proximally, but forms a wide fin in the distal half of the club, the attachment of which is typically displaced toward the dorsal edge of the inner surface (Figure 94 on p. 204).

(177)

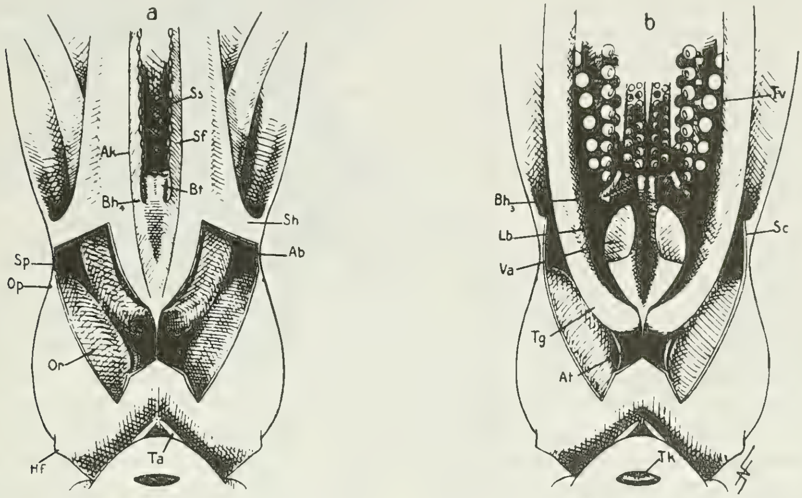


FIGURE 76. Base of the tentacle in the Loliginidae. Two phases of a preparation of Alloteuthis media (2×). Compare with Plate II, Figure 3, and Figures 81, 82 on p. 183. Note the median insertion of the tentacle stalks behind the base of the ventral arms which is typical for all recent Decapoda, and the connection of the invaginated base (Tg) with the surface by an elastic skin fold (Lb). In its margin passes the efferent vein of the tentacle, which joins the circumoral collecting vessel at the level of the other arm veins (at the primary position). In contrast to the typical Sepioidea (Figure 322), the tentacle pockets are characteristically widened, with the tendency to expose the muscular bases of the arms and detach them from the other organs of the head.

Sp — slit between eye and bases of arms; Op — orbital pore; Or — wall of orbital chamber adjacent to tentacle pocket; Hf — third longitudinal neck fold; Tr — funnel adductor; Bh_4 — buccal attachment of fourth buccal pillar; Ak — outer median edge of fourth arm; Ss — its protective seam; Sf — its median surface; Bt — buccal funnel (4th pillar); Sh — membrane between the V and LV arms; Ab — base of LV arm; Bh_3 — third buccal attachment; Lb — attaching ligament; Va — base of removed V arm; Tg — base of tentacle; At — muscular support of arm; Sc — cut surface of membrane between V and LV arms; Tv — tentacle vein; Tk — funnel valve.

The narrow inner side of the arms bears two rows of suckers which are rather uniform and begin close to the base. The suckers are clearly claw-shaped, with a markedly eccentric stalk and strong teeth at the distal margin of the horny ring. The teeth decrease in size toward the lateral margin and are represented only by small tubercles at the proximal margin (Plate XII, Figure 1; Plate XIII, Figure 7).

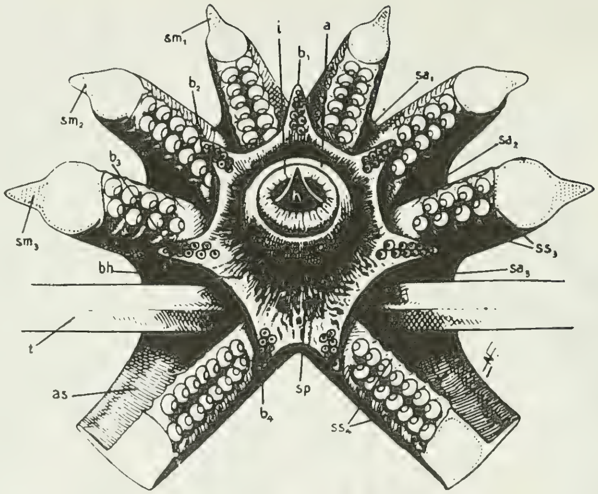
The rows of suckers are accompanied by typical protective margins and the number of supports is equal to that of suckers in the adjacent row. The rows disappear at the base of the arms without direct connection with

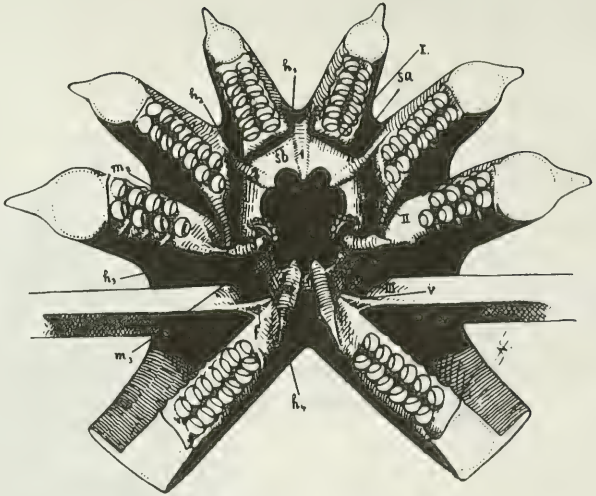
the buccal funnel. The margins are much larger on the ventral inner edges than on the dorsal edges, especially on the second and third pair of arms,
177 as we assumed already for Protodecapus (p. 116).

The tentacle clubs bear 4 rows of suckers; the primary biserial arrangement is present only near the base. The area occupied by the small proximal suckers is the carpal part, since a distinct stalk part is absent and there follows a rapidly widening and then tapering hand part. The suckers of the hand part are much larger, especially on the inner rows (Figure 94 on p. 204), which have a radial structure and are only slightly but uniformly toothed in contrast to those of the arms. Distal to the hand part is a narrow distal part, which in preserved specimens is always curved dorsally, toward the swimming margin. The distal part bears small suckers, those of the ventral row being the largest. The apex of the club forms a typical terminal part, with a few transverse rows of small flat suckers which are situated on an especially solid and rigid "terminal plate." This is characteristically bent upward and inward and apparently serves for the initial grasping of the prey (cf. p. 120).

178 The protective margins of the tentacle clubs are characteristic. They are very wide in the hand part and have the same number of supports as the number of suckers in both rows of the adjacent side. The supports, however, are more strongly developed before the marginal suckers, but not equally on the two protective margins. The supports of the dorsal margins have the usual form, those of the ventral margins are widened like a spatula laterally, with fanwise radiating muscle bundles, but only on the hand part of the club (Figure 94 on p. 204). A ridge continuing the ventral edge is present near the base of the tentacle stalk. It contains the efferent vein of the arm, which extends to the buccal sinus. It is situated at the margin of a typical ligament (Protodecapus, p. 119) which makes it independent from the invagination of the tentacle base (Figures 77, 78 on p. 179). The attachment of the tentacle stalks is typical for all Decapoda: the stalks are contiguous in the middle behind the bases of the ventral arms and are situated in the large, tentacle pockets. Although the tentacles of the Loliginidae are free between the other arms, as in the Oegopsida, these pockets are very large and have the character of true cephalic cavities, because they do not contain the tentacles (Figure 76 on p. 177). They expose not only the tentacle base but also parts of the bases of the lateroventral arms and the inner wall of the eye chamber. A median slit from the eye to the upper wall of the head separates the complex of the arm bases from the head. The orbital cavity is naturally separated from this slit by a thin wall which consists of mesenchyme and of the epidermis of both cavities (Figure 76, Or). The free arm support persists as a small muscle mass in the middle between the pockets of each side (Figure 76, b, At). It is connected with the eyes by thin superficial layers so that the internal cavities (eye chamber, orbital cavity, tentacle pockets, buccal pockets) are covered.

A view of the mouth area of a specimen with spread arms (Figures 77, 78 on p. 179) shows that the bases of the arms are connected by large muscular cords which are visible already on the surface. They surround the buccal mass and especially the buccal funnel, so that the adductors of the D arms end inside the base of the second arms, and those of the second arms inside the base of the third pair, which in turn extend toward the 4th pair. The angle formed at the junction of the bases of the third and fourth pair is occupied by the fastening ligament, i. e. the rudimentary adductor of the tentacle stalk.





Mouth region of Loligo vulgaris with spread bases of arms (cf. Figure 45 on p. 119). Natural size.

FIGURE 77. The buccal pillars (oral arms) are also spread. Note the form of the buccal cone from which projects the apex of the lower jaw, surrounded by the papillose inner lip and the membranous, slightly wrinkled outer lip (cf. p. 65). The cone projects only slightly, but it may protrude much further. Around the cone is the buccal funnel with its 7 points, connected by a rugose membrane. The suckers are biserial. The relationships between buccal funnel and outer arms are shown in Figure 78.

k – apex of lower jaw; i – inner lip; a – outer lip; b_{1-4} – buccal points; sm_{1-3} – swimming margins between the 3 upper arms; bh – buccal membrane; t – tentacle stalk; as – outer margin; sp – place for the reception of the spermatophore in the female; $ss_{3,4}$ – protective margins; sa_{1-3} – connections of protective membrane.

FIGURE 78. The same preparation with contracted buccal pillars (oral arms), which are well delimited on the outside from the connecting membrane. Note connection between buccal pillars and arm bases. Because of its development from two pillars, the dorsal pillar has a double connection. Note the 6 entrances to the buccal pockets, the whole extent of which is shown in Figure 79.

h_{1-4} – attachment of buccal pillars; 1–4 – buccal pillars; sb – protective membrane between two pillars; I-IV – buccal pockets; sa – protective membrane between upper arms; v – tentacle vein; f – fastening ligament; m_2 and m_3 – adductors of second and third arms.

The buccal funnel (Figure 77) shows the typical characters of the Decapoda, Teuthoidea and Metateuthoidea. The 7 pillars and points bear two inner rows of suckers like those on the arms.* The pillars or oral
179 arms (Figure 78) are rooted at the base of the arms. The dorsal pillar is situated between the dorsal arms, the dorsolateral between the first and second arm on each side, the lateroventral at the ventral inner edge of the base of the third arm, the ventral at the base of the fourth arm near the median inner edge. Small folds ("fastenings") pass outward from the bases of the 7 pillars but do not reach the protective margins of the arms. The inner side of the buccal funnel or the membrane connecting the pillars is coarsely wrinkled and folded. These conditions are typical for all recent Decapoda (p. 122).

180

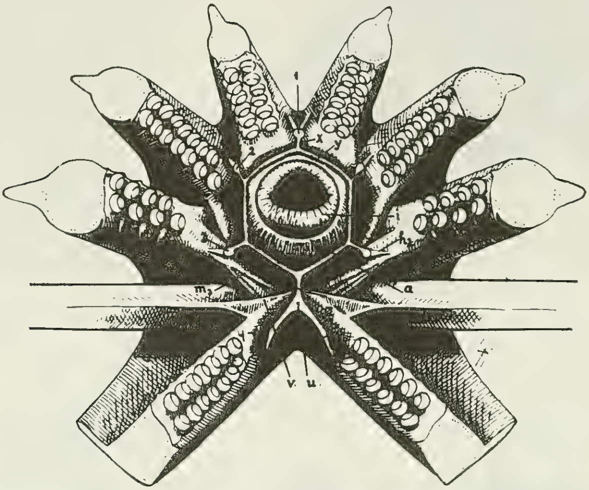


FIGURE 79. Mouth region of a male Loligo vulgaris. Same preparation as in Figures 77 and 78 but with the buccal funnel removed, except for the adjacent parts. The buccal pockets are expanded into the head between arm bases and mouth mass, making this as movable as the arm bases by the deepening of the tentacle pockets (p. 177). The attachment of the buccal membrane is pushed toward the mouth cone and assumes the hexagonal form typical for all recent Teuthoidea (Metateuthoidea) (p. 159). The buccal funnel consisting of 6 parts (cf. Plate III, Figure 2) appears therewith prepared. Note also the structure of the arms: swimming margins, protective margins, protective membranes, the muscular pillars between them, the insertion of the tentacles and the base of the fastening ligaments.

1–4 – bases of buccal pillars (cut); M_3, v, i, a, h_3 – as in Figure 77; y – attachment of buccal membrane on mouth cone; x – connection between buccal membrane and dorsal pillar; z – similar connection with the ventral pillars; u – predestined site for the fusion of the two ventral pillars.

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* I formerly believed that I was the first to recognize that the buccal pillars are rudimentary arms (Naef, 1912, Cephalop., p. 248); at any rate, I based this view in the whole context of the morphology of Cephalopoda on a comparison with Nautilus. I found later that Vialleton (1885, R.C., Paris) expressed the same view at the end of a small article: "si l'on tient compte de la masse musculaire des lobes, de la présence des ventouses, et surtout de l'existence dans chacun d'eux d'un cordon ganglionnaire analogue aux nerfs des bras et ayant avec eux une origine commune, on voit que tout nous porte à regarder ces lobes comme de véritables petits bras rudimentaires, et par suite, à rapporter la membrane buccale à un cercle de bras dans lequel la membrane interbrachiale serait très développée par rapport aux bras eux-mêmes."

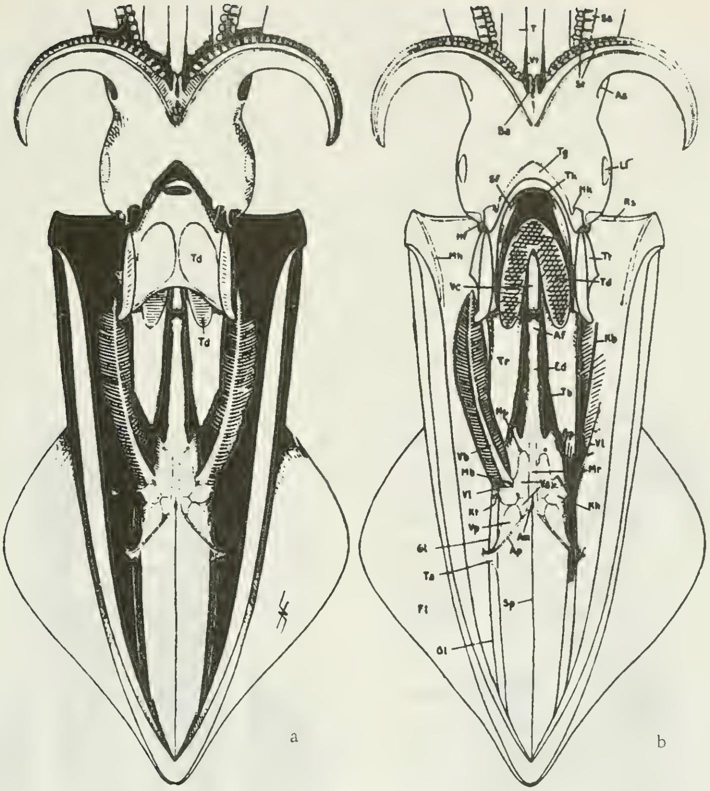

FIGURE 80. Mantle cavity of Loligo vulgaris. Young male 2×. a) Mantle cut in the middle and spread. b) Same preparation after removal of the anterior wall of the funnel, one gill (cut at the base), a gill ligament (Kb) and parts of the posterior pallial artery and vein passing the margin of the gladius. Note in Figure a: the relation of the fastening ligament to the ventral buccal pillars and the base of the ventral arms while the tentacles are extended; the position of the folded over protective margins, the structure of the funnel pit, the anterior transverse fold and the third longitudinal fold of the "neck"; the outer form of the funnel and the funnel valve in its opening, the form of the funnel cartilage; the position (dotted) of the translucent lower parts of the funnel gland (Td), the bilobed anterior part of which is visible in Figure b, on which the funnel valve is also visible; the funnel pockets (Tt); funnel retractors (Tr); structure of anal papilla (Af); vena cava (Vc) median and anterior to the anal papilla; ink sac (Tb), half-covered by the hind intestine in its typical position; the renal pores in the form of small papillae between which the musculus rectus abdominis is visible (Mr) (dotted), which ends near the median pallial artery (Am); the anterior part of the venous appendages (Va), which are situated near this muscle and belong to the venous branches; the smaller posterior part of the appendages, which belongs to the base of the posterior pallial veins; the branchial hearts (Kh), visible through the base of the gills; the typical structure of the gills with the small, superficial branchial retractor (Mb) at the base of the efferent vessel; the posterior opening of the branchial pockets (Kt) on the exposed margin of the gladius (Cl), which is covered only by a remnant of the primary mantle; the posterior pallial vein (Vp) and posterior pallial artery (Ap), which extend to the margin of the gladius further posteriorly; the median pallial artery (Am) at the anterior margin of the median pallial septum; the linear mantle bonds (Mh) on the mantle. Figure b illustrates the structure of the inner side of the funnel: the form of the funnel gland (Td) and funnel valve (Tk), which continues in a powerful muscular layer (Sf) on the ventral side of the funnel. Also shown are the area of the gill roots with the free passage (Kt) from the pocket of the gill root into the posterior part of the mantle cavity, which is bridged by the gill root.

Ss – protective margin; T – tentacle stalk; Vt – fastening ligament with vein of tentacle; Ba – ventral buccal pillar; St – supports of protective margin; As – lateral margin of the V arm; Tg – funnel pit; Hk – lateral tubercle; Li – lens of eye; Rs – marginal seam of mantle; Gp – genital process; Vl – lateral pallial vein; Vb – branchial vein; Ta – pocket formed by the skin fold which permits the passage of the posterior mantle vessels into the mantle; Fl – fins.

(183)

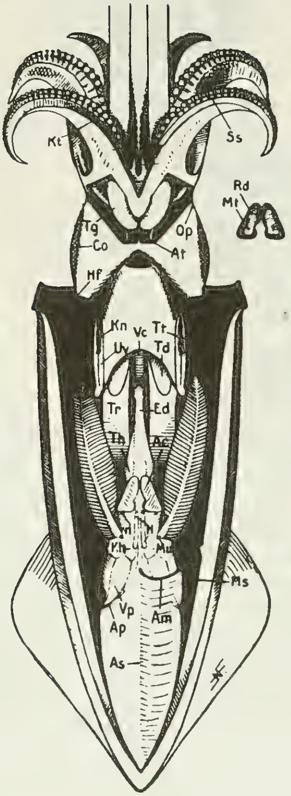
Kt
Ss
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FIGURE 81.

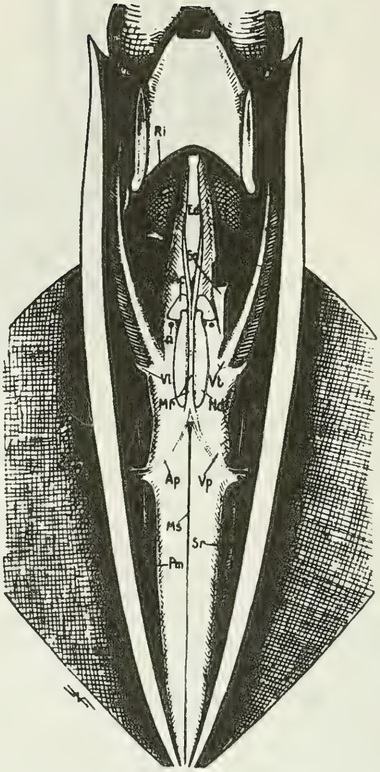
Ri
Ed
Vl
Vt
Mf
Hd
Ap
Vp
Ms
Sr
Pm

FIGURE 82.

(183)

Situs of mantle cavity of young females of Loligo vulgaris

FIGURE 81. Younger animal, natural size. The tentacle pockets are opened as in Figure 76; the mantle cavity is opened and spread. The median pallial septum (Ms) was left intact and pulled aside. The general arrangement shows the typical condition in the Metateuthoidea (p. 140). Note particularly the "anlagen" of the genital organs (N, Ac). The nidamental glands (N) are flat, narrow sacs between the gill roots, near the middle. Before their openings are the large accessory glands in the form of raised, sharply delimited epithelial growths with characteristic outline and an indentation on the inner side, at the point reached by the anterior end of the nidamental glands (Figure 82). The diagram in the upper right near the main figure shows that the median zone is covered with the small openings of the gland canaliculi, while the marginal part still shows the systems of ridges which produce the canaliculi (cf. p. 125); the openings are actually much smaller and denser. The large gland surfaces lie anterior to the renal pores (Figure 48!), as is typical for the Teuthoidea and in contrast to the Sepioidea (cf. also Ctenopteryx and the Sepiolidae!).

Kt — median outer edge; Ss — protective margin of a ventral arm; Tg — tentacle root; Co — cornea; Op — point of orbital pore; At — arm support; Hf — neck fold; Kn — cartilaginous and Uv — noncartilaginous part of funnel support; Vc — vena cava; Tt — funnel pocket; Td — funnel gland; Tr — funnel retractor; Ed — hind intestine; Th — ink sac; Ac — accessory nidamental gland; N — nidamental gland; Kh — branchial heart; Mu — superficial branchial retractor; Am — median pallial artery; Ap — posterior pallial artery; Vp — posterior pallial vein; As — attachment of pallial septum (Ms) on the body; Mt and Rd — middle and marginal parts of accessory gland (the former with gland pores, the latter with gland ridges which produce the pores).

FIGURE 82. Older animal, half natural size. Ventral side of muscular mantle removed; the other parts slightly spread. Organs in the natural position. Note the further development of the female genitalia in comparison with Figure 81. The nidamental glands have become longer and wider posteriorly and anteriorly; they already show a typical internal differentiation. The openings of the glands are displaced toward the accessory glands, creating the impression that their secretion will be combined with that of the accessory glands which have become relatively smaller; the formation of gland canaliculi has ceased and the openings of the existing canaliculi are concentrated in the middle of the gland, leaving only the blind ends of the distal canaliculi in the marginal part. The genital process (Go) has grown far toward the anus along the body; it shows a wide, pocketlike opening, the margins of which are attached to the body on the inner side. A fold projecting from above divides this opening incompletely into two parts.

Ri — funnel retractor; Ed — hind intestine; Go — genital opening; Ac — accessory gland; n — renal papilla; Vl — lateral pallial vein; Vb — branchial vein; Mr — musculus rectus abdominis; Nd — nidamental gland; Vp — posterior pallial vein; Ap — posterior pallial artery; Ms — pallial septum; Sr — shell margin; Pm — primary mantle.

The development of the buccal pockets is of particular interest (Figures 77, 78, 79). All six pockets penetrate deeply between the arm bases and the buccal mass, making these parts independent of each other in their movement. In this respect the buccal pockets have a similar function as the tentacle pockets (p. 121). Their expansion removes the basal part of the buccal membrane from the supporting pillars and pushes them toward the mouth cone, leaving only membranous bridges (Figure 79, x) between the pillars and protective membrane, and a single forked bridge for both ventral pillars, between which there is no pocket, while the adjacent pockets meet in the middle before the base of the tentacle. This condition, which is typical for all Metateuthoidea (p. 159), arises during postembryonic development and is not a character of the different types (cf. e.g. Ommatostrephidae). Further metamorphoses may take place (Octopodoteuthis, Pyroteuthis, Sthenoteuthis). In particular, the connection between the ventral buccal pillars and the buccal membrane is apparently a preparation for their fusion, as it was assumed for the dorsal pillars in the prototype of the Decapoda (p. 122) and which is actually observed in the ontogênesis (Histioteuthis, Plate III, Figure 2; cf. Vol. II, Plate XXI). The sexpartite connection with the mouth cone (Figure 79) then replaces the sexpartite structure of the entire buccal funnel.

182 The funnel apparatus shows most of the typical characters of the Decapoda. As in Metateuthis (p. 152), however, the neck bond is narrowed and characteristically slipper-shaped in the Loliginidae (Figure 85 on p. 185). The funnel apparatus has a thin median groove with flat ridges on each side. The funnel tube is short and strong. The funnel supports (Figure 82) are characteristically long and narrow, with a slightly pointed anterior and blunt posterior end which is curved outward. The funnel supports extend to the anterior margin of the funnel pockets. Their anterior and middle parts form a shallow depression; its posterior part is rather flat. The anterior half of the funnel support is cartilaginous ("funnel cartilage") and appears darker in most preparations (Plate II, Figure 1; Figure 95). The funnel contains a typical valve and a gland the dorsal part of which projects slightly from the posterior opening of the funnel (Figure 80 on p. 181).

(184)

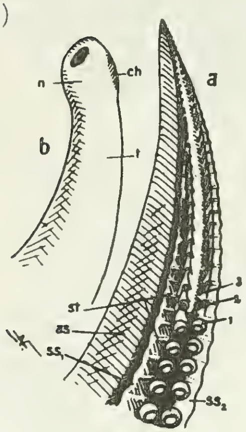

FIGURE 83. Hectocotylus of Loligo forbesi. a) Natural size. Apex of arm with 5 pairs of normal suckers followed by numerous abnormal, toothless suckers on pillarlike supports, without differentiated stalk. b) Same under higher magnification. The outer side of the sucker shows a dark spot, probably a chromatophore, which is commonly present at this point.

ss_1 – outer protective margin; ss_2 – median protective margin; as – outer margin; st – protective support of margin; 1 – normal distal sucker; 2 – modified sucker (transitional form); 3 – long support of a completely modified sucker; t – support; n – sucker; ch – chromatophore.

The funnel retractors project as massive cords into the mantle cavity. They are free, which we must assume also for Protodibranchus, Protodecapus, Prototeuthis and Metateuthis. A deep groove separates the funnel retractors (Figures 84, 85 on p. 185) from the cephalopodial retractors, giving them room for action. The two muscles unite only before their origin on the shell (Figure 73 on p. 173).

The situs of the mantle cavity shows in general the characters known from Metateuthis and still closely resembles the type of all Decapoda. The condition of the gill root pockets is characteristic and is illustrated in greater detail in Figure 80 on p. 181. As we shall also see in the Ommatostrephidae, the pockets open posteriorly in the mantle cavity, but this appears only during the postembryonic development. This open passage behind the origin of the funnel retractors effects that the gill roots form a bridge over the margin of the gladius (Figure 80, b), to be attached on the muscular mantle by the gill ligament. The lateral pallial vein uses the same bridge to pass to the mantle. The posterior pallial vein and artery pass in a skin fold to the muscular mantle, over the projecting margin of the shell, detaching these vessels from the primary mantle in which they open in Nautilus. This fold forms a characteristic pocket which extends posteriorly under the vessels along the gladius. Its penetration at this point is probably only a matter of time, so that in the descendants of the recent Loliginidae also these vessels will move freely over the margin of the gladius toward the mantle, like the lateral pallial vein (cf. Figure 95).

The whole complex of the mantle cavity of the Loliginidae is rather regularly symmetrical, in contrast to the numerous asymmetries in the Oegopsida. Thus, the ink sac is situated in the middle above the hind intestine; the venous appendages, which are visible through the skin, are symmetrically situated, etc. On the other hand, the genital process is invariably situated on the left (Figure 82); it develops entirely in the gill root, but grows later more or less toward the anus, along the body wall, but its terminal part remains free (Figure 80 on p. 181 and Figure 95 on p. 205).

184 The jaws and radula of Loliginidae show no special characters. The jaws are of the typical character of Decapoda, the radula the character of the Dibranchiata (pp. 122 and 67; cf. Plates XIV and XVII).

The Loliginidae and therefore probably also Protololigo show a marked sexual dimorphism which is not restricted to the sexual characters but is also distinctly expressed in the external habitus. The males are always much slenderer than the females (cf. Loligo vulgaris, pp. 199 and 200; also Alloteuthis subulata); the flag of the gladius is therefore much narrower in the male (p. 201). The difference in the proportions is due to a large extent to the relative length of the mantle sac which is much longer in males than in females of the same size. This difference only appears later in the development, when the animal becomes mature. I consider as typical the condition in Loligo vulgaris (see p. 200). Hectocotylization occupies the left ventral arm as is typical for all Decapoda (I found only one specimen of Alloteuthis media with a hectocotylized right arm) and is restricted to the apex of the arm. The arm develops abnormal suckers which are often wrongly considered simple "papillae." The sucker supports are strongly elongated, pillar-shaped; they taper distally and pass without a differentiated stalk into a small, sessile,

(185)

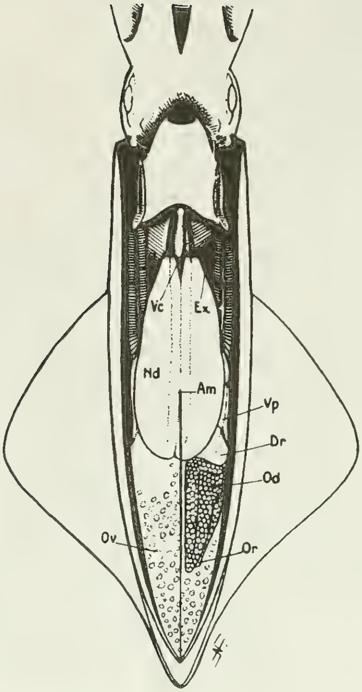
Vc
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FIGURE 84.

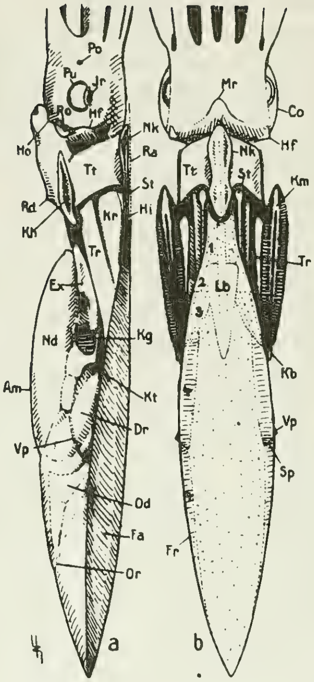
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FIGURE 85.

Situs of mantle cavity of a mature female of Loligo vulgaris (A drawing of the whole specimen is given in Figure 92 on p. 200; Figure 69 shows the shell situs of the same specimen). Half natural size

FIGURE 84. Ventral side of mantle removed; the other parts left in their natural position. The enormous, fully functional nidamental glands (Nd) are striking. They have advanced anteriorly over the accessory glands, to which their openings are directed; they surround the median pallial artery (Am) posteriorly. A thin longitudinal line (dotted) on each side marks an inner slit where the gland lamellae meet. The opening of the oviduct (Ex) is directed toward the gland opening on the left. Thus, the oviduct and the oviduct gland (Dr) inside it can function together with the nidamental and accessory glands in oviposition. The filled proximal part of the oviduct (Od) with the opening into the coelom (Or) are visible through the skin in the upper part of the visceral sac.

Ov — ovary; Vp — lateral pallial vein; Vc — vena cava.

FIGURE 85. Same specimen, without shell and mantle. a) left side; b) dorsal. The position in the shell can be imagined from Figure b (cf. Figure 69 on p. 169); the posterior part of the body covers exactly the gladius flag, except in gravid or fully fed specimens (Figure 82). The posterior part of the body is fused with the gladius (or shell sac) only in the dotted zone; the rest of the gladius is situated as shown in Figure 73. The attachment of the gill ligament (Kb) to the mantle is best understood by comparison with Figure 80 and also the passage of the lateral pallial vein into the mantle. The more densely dotted anterior zone corresponds to the origin of the cephalopodial (1, 2) and funnel retractors on the shell. Comparison with Figure 69 on p. 169 shows the position of the stellate ganglia (St) and the fin nerves extending from them posteriorly in the connection between body and shell; also the articulation of the neck bond (Nk) with the anterior part of the gladius. The normal position of the anterior margin (Mr) of the mantle is marked (dotted) in the middle of the vertex. Note in Figure a: bases of arms; orbital pore (Po), pupil (Pu; translucent); neck fold (Hf) and olfactory organ (Ro). In the funnel apparatus: funnel support (Kh), attachment of funnel pockets (Tt), connection of neck (Nk) with the anterior end of the gladius (Ra; dotted). In the posterior part of the body: the dorsal side, adjacent to the gladius, simplified; the shell epithelium (Fa) is shown uniformly, but its margin is not firmly fused posteriorly with the body but belongs to a rest of the primary mantle (Figure 71 on p. 170). Further are shown: the course of the cephalopodial retractors (Kr) and the funnel retractors (Tr), separated from it by a deep incision; nidamental gland (Nd), opposite the funnel-shaped opening (Ex) of the oviduct (Od, Dr), which is exposed by removal of the greater part of the gills; the stump of the gills (Kg) and the line of their fusion with the mantle, parallel to the shell margin.

Ir — iris flap; Hö — tubercle corresponding to the 4th longitudinal neck fold; Rd — posterior margin of funnel; Ra — position of rhachis; Hi — posterior end of neck cartilage; Kt — posterior opening of pocket of gill base; Vp — posterior pallial vein; Or — entrance to oviduct; Fr — free margin of inner shell epithelium; Sp — fold at passage of posterior pallial vein into the muscular mantle; Km — gill.

toothless sucker, specialized for the holding of the spermatophores and without other function (Figure 83, b). The number of these modified suckers varies greatly, there are over 50 in the larger specimens of Loligo.

The number of the suckers situated before the heteromorphous part of the arm is of systematic importance, especially that of the inner (median) rows, although these also vary in some species, and even more in the family (9–30). There are apparently no normal suckers on the hectocotylus in Loliolus.

186

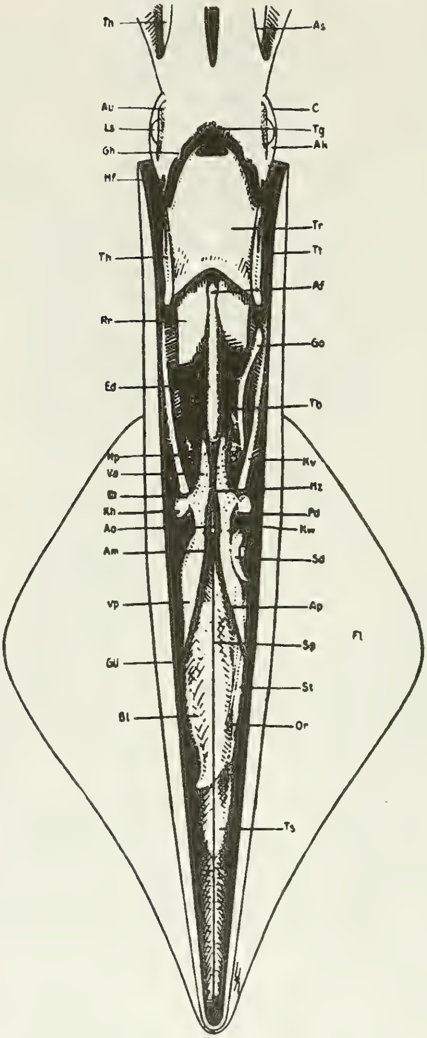

FIGURE 86. Situs of mantle cavity of the mature male shown in Figure 91 on p. 199. Half natural size. Fresh preparation. Note: hind intestine (Ed) and ink sac (Tb); genital process (Go), proximal to it the gonoduct with the spermatophore gland (Sd) situated behind the branchial heart; opening into the coelom (Or); apex of spermatophore pocket (St); branchial hearts (Kh) and their appendages (Pd); venous appendages (Va) in the renal sacs; heart (Hz) with the posterior aorta (Ao); posterior pallial artery (Ap), median pallial artery (Am); posterior pallial vein (Vp); renal openings (Np); caecum (Bl); testis (Ts).

Kw – point of perforation of the branchial pocket; Kv – branchial vein; Tr – funnel tube; Ak – eye chamber; Tg – funnel pit; C – cornea; As – lateral margin of arm V; Tn – tentacle stalk; An – eyeball; Ls – lens; Gh – lateral tubercle; Hf – third longitudinal neck fold; Th – funnel support; Rt – funnel retractor; Rt – superficial branchial retractor (ligament); Ao – aorta; Gü – passage of posterior pallial vessels from body into mantle and fins.

The genital processes of male Loliginidae are apparently situated on the body wall, as in the Sepiolidae, not in the genital pocket as was assumed for the ancestral form and observed in the Oegopsida. This results from the fact that the opening of the genital pocket closely surrounds the genital organ and is fused with it during postembryonic development, leaving a narrow, indistinct pore (Figure 35 on p. 105). This condition persists in Loligo pealei (Williams, 1909) and probably also in other forms which have not been studied in this respect. In the species I have examined the genital pocket is closed completely at an early stage.

The females have typical accessory and true nidamental glands, which are generally absent in the male. However, males of Loligo forbesi have accessory glands (see p. 206) as was observed also by Wülker (1912)

187 The nidamental glands are situated early in postembryonic development in their typical position near the exit of the posterior pallial veins from the renal sacs (Figure 35 on p. 105). They grow anteriorly in the form of narrow pockets in which the gland lamellae develop (Figures 81, 82 on p. 183). The accessory glands are also displaced anteriorly; at any rate, they no longer extend posteriorly into the renal papillae as was assumed for Protodecapus (cf. Sepiidae and Sepiolidae!) (Figures 48, 49 on p. 125) but are situated in front of them, close together in the middle. In young animals they reach their maximal size shown in Figure 81 but their growth lags later, and they become relatively smaller (Figure 82). On the other hand, the nidamental glands grow continuously and their anterior end forms a papilla at the opening which covers the corresponding accessory gland completely (Figure 84). The nidamental glands extend also posteriorly, enclosing the median pallial artery between them in mature animals.

c. TYPICAL POSTEMBRYONIC DEVELOPMENT

Figure 87 shows a median section through an older embryo (diagrammatic) for orientation on the morphology of very young Loliginidae. The drawing also illustrates the condition in the Teuthoidea and Decapoda in general. Compare for explanation also Volume II.

188 The postembryonic development of Loliginidae shows remarkable characteristics. Figure 88 shows the habitus of a newly hatched animal. It is based on Loligo vulgaris, but it also shows the typical characters of other species and genera. The only marked variations are found in young Sepioteuthis, in which the fins are not yet fused in a narrow ridge at the posterior end (Wülker, 1913). The fins show the characters typical of young Decapoda and especially Teuthoidea: they are terminal, rounded, laterally projecting lobes which are much wider than their base on the mantle (cf. also Figure 60 on p. 143). Hoyle's organ (Vol. II, Plate VII, Figures 87 and 165) is completely preserved at hatching but disappears rapidly later. The mantle sac of these very young stages is still very short. In extended state, it is almost as wide as long, and capable of movement, to which the funnel apparatus is adapted. The animals swim rapidly, in jerks and leaps, their posterior end obliquely turned upward. The neck bond is already distinct, but the funnel supports are not yet sharply delimited. At any rate,

the muscular mantle already adheres to the funnel at their position, and a distinctly bordered stripe appears on each side of the funnel soon after 189 hatching. External funnel adductors are present already at this stage. Except for the closing of the primary lid into a cornea, the head shows the typical characters of the larvae of Decapoda: it is dorsoventrally flattened, the eyes are directed anteriorly, and the flat, oval olfactory papillae are situated on the ventral side.

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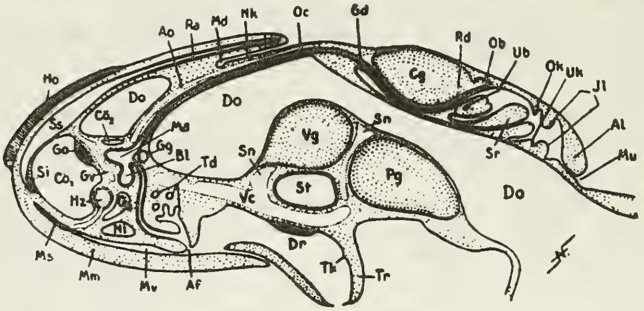

FIGURE 87. Median section through an older embryo of Loligo vulgaris (diagrammatic). Approximately 30×.

Ho — Hoyle's organ (median part); Ss — shell sac; Go — "anlage" of gonad; Si — rudiment of siphuncle; Cö$_1$, Cö$_2$, Cö$_3$ — parts of coelom; Gv — genital vein; Hz — heart; Ms — mantle septum; Mm — muscular mantle; Mv — mantle cavity (ventral); Af — anus; Ni — kidneys; Do — yolk; Ma — stomach; Gg — gastric ganglion; Bl — caecum; Td — ink gland; Vc — vena cava; Dr — funnel gland; Tk — funnel valve ("anlage") Tr — funnel; St — statocyst; Sn — blood sinus; Vg — visceral ganglion; Pd — pedal ganglion; Cg — cerebral ganglion; Sr — subradular organ; Ao — anterior aorta; Ra — rhachis part of shell sac; Md — dorsal mantle cavity; Nk — neck cartilage; Oe — esophagus; Gd — poison gland; Rd — sac of radula; Ob — upper buccal ganglion; Ub — lower buccal ganglion; Ok — upper jaw; Uk — lower jaw; Il — inner lip; Al — outer lip; Mu — mouth.

Compare with Figure 59 on p. 142. This is the typical structure of an embryo of Dibranchiata, but the cone part of the shell sac is already flattened and reduced, the siphuncle is hardly indicated, and the shell sac is divided into flag (or cone) part and rhachis (or proostracum) part. This section is important for the morphological interpretation of such stages and shows a very instructive picture of the topography of Dibranchiata.

The yolk sac is still present as a small remnant between the eyes. It falls off readily and is eaten by the young animal, as I observed in young Argonauta (q. v.). The lip membranes are already normal; the buccal funnel is just beginning to develop and its supports (the "oral arms") still form small papillae, naturally still without suckers. The arms also bear only a few (proximal!) suckers at this stage, some of them still rudimentary, in the form of round warts (Figure 88b). Only the tentacles have well-developed suckers. The proportions of the arms differ markedly from those of the Oegopsida. In newly hatched oegopsid larvae, the 3rd and 4th pair of arms either appear much later or are small, papilliform "anlagen," but they are the strongest arms in the Loliginidae; in Loligo vulgaris, the third arm has at least 3, the fourth at least 2 suckers. On the other hand, the two dorsal pairs are only stumps; the D arms are mere warts without suckers, while the DL arms bear a rudimentary sucker.*

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* The typical character of this juvenile stage is explained by a comparison with Figure 147. The young larva shown resembles our Myopsida so strikingly that even the nonspecialist easily recognizes the close relationship between the two groups. Compare also Plate IV, Figure 2, or Figure 140 on p. 290, i.e. young Enoploteuthidae.

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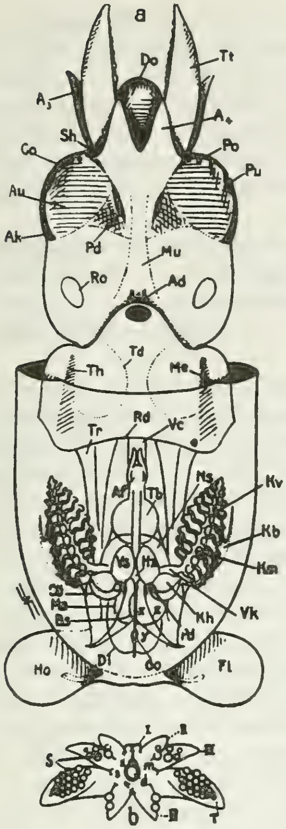

FIGURE 88. a) Newly hatched Loligo vulgaris (18×). Drawing of the living animal, which is quite transparent, completed from a preserved specimen. b) Arms of an older embryo, just before hatching, after removal of the yolk sac attached at d. The mouth (m) is situated above the wound. Suckers are present only in small numbers and are absent at this stage on the retarded, stumpy D — arms. The buccal points (1–4) are still only small flat papillae. 1–4 — arms; r — tentacles.

The main figure shows the small remnant of the yolk sac (Do) between the arms; the small, stumpy, pointed arms (A_3, A_4), above which the tentacles (Tt) project; protective membrane (Sh) situated between the third and fourth arm and surrounding the still shallow tentacle pocket; the eyeball (Au) in the enclosed orbit (Ak, hatched); orbital pore (Po); cornea (Co); olfactory tubercles (Ro), still in the form of flat warts on the ventral side of the head; funnel adductors (Ad); the funnel apparatus with the developing funnel supports (Th) and the translucent ventral parts of the funnel gland (Td/; anal papilla (Af); vena cava (Vc); hind intestine and ink sac (Tb); funnel retractors (Tr); the gills with the alternating, undulate branchial lamella, branchial spleen (Km); the gill ligament (Kb), which is still restricted to the proximal part of the organ; the branchial heart (Kh) with its appendages (Pd); the sac-shaped venous branches (Vs), receiving posteriorly the posterior pallial veins (z); posterior aorta (x) and its branching into the median pallial artery and posterior pallial artery (y); the rounded, laterally projecting fins (Fl), through which the lateral branches of Hoyle's organ (Ho) are visible (dotted).

Go — "anlage" of gonads; Di — internal yolk sac; Bs — caecum; Ma — stomach; Cö — coelomic pockets for the branchial heart; Vk — atrium of heart; Hz — heart chamber; Kv — branchial vein; Ns — renal sac; Rd — posterior margin of funnel; Me — ventral corner of mantle; Mu — straight, superficial cephalic muscle; Pd — stalk part of eye inside the eye chamber; Pu — pupil.

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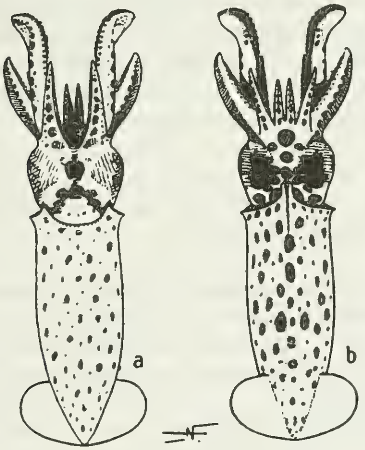

FIGURE 89. Typical juvenile stage of Loliginidae, in this case Alloteuthis media (2×). The ancestral form probably still lacked Loligo-like characters, like the sharp dorsomedian process of the mantle, and had instead a simple corner (Figure 114).

a — ventral; b — dorsal.

The end of the arms grows rapidly, adding suckers so that one sucker is always displaced to the right and the next to the left. A uniserial arrangement is therefore never distinct. A similar development takes place on the tentacles, but here pairs of suckers are displaced so that 4 rows are formed. On the outer edges of the arms, the swimming margins and protective margins are at first quite rudimentary but develop rapidly, and a short time later the young larvae already show the typical characters of the family (cf. Plate I). Above all, the fins gradually develop to the definitive condition. The width at the base increases and their relative width decreases. The fins of the youngest stages are flapping lobes which closely resemble those of the fossil Prototeuthoidea (Figure 60 on p. 143). The fins develop into muscular plates which move in specific, undulate movements, maintain the equilibrium and act as rudder and for active movement. This is the stage shown in Figure 89 (see also Plates I and II).

The mantle sac becomes slenderer, the typical corners at its free margin become more distinct, and the funnel incision becomes deeper. Near the olfactory organ (p. 173) appear the neck folds, and the buccal funnel develops
190 between the arms. The 7 points remain at first short; their suckers appear much later and may not develop at all.

These nektonic forms can naturally not be reared in our small tanks. Our postembryonic stages, mainly of Loligo vulgaris, were obtained from plankton samples in which they are not common. These agile animals with sharp vision easily escape from plankton nets, like all nektonic cephalopods. The young forms of different species are very similar. A stage as that shown in Figure 89 is representative of the development of at least all Logininae;* a more exact identification of a similar or younger stage is usually impossible, unless the occurrence of a form provides some definite evidence. For example, I know that the specimen illustrated in Figure 89 belongs to Alloteuthis media, because it was accompanied by developmental stages of this species, and the coloration and the distribution of chromatophores are characteristic for the species, although I do not consider them as systematically applicable. Differences of size between the various stages are also useless. There are very small and very large varieties of Loligo vulgaris which differ already in the embryonic period so markedly that the smallest may easily be confused with Alloteuthis.

The interpretation of the stage illustrated in Figure 89 applies also to Protololigo, with the same qualification. However, the genus and also the species can be determined relatively easily as only a small number of species come into consideration (4 in Naples). The transition to the conditions shown in Figure 68 requires no further explanation.

191 d. VARIATION OF THE TYPE OF LOLIGINIDAE

The family Loliginidae contains numerous species and their determination and classification in natural genera are rather difficult. The species show a marked variation so that there are transitions between the groups. The presence of intermediate species often bridges contrasts which might otherwise lead to the establishment of genera.

The family consists of 3 distinct groups which I consider as subfamilies; species resembling Sepioteuthis, Loligo and Loliolus.

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* According to the illustrations by Wülker (1913), the Sepioteuthidae can be distinguished easily and at a very early stage from the Loligo-like forms (cf. also d'Orbigny, 1839, Plate 10, Figure 6).

Synopsis. I. Small Loliginidae without a markedly projecting tooth (Figure 89) in the middle of the dorsal margin of the mantle; without a fringed skin fold at the margin of the large suckers on the tentacles; without externally visible funnel adductors; fins heart-shaped, blunt posteriorly, leaving the anterior half of the mantle sac free. Subfamily Loliolinae nov. (Lolius typus Steenstr., 1856, L. affinis Steenstr., 1856, L. investigatorius Goodrich, 1896).

II. Loliginidae without a distinct tooth in the middle of the dorsal margin, of the mantle, which forms only a blunt corner; funnel adductors more or less distinct; fins longitudinally rhomboidal or oval, and extending almost along the whole mantle sac. Subfamily Sepioteuthinae nov., (Sepioteuthis (cf. Wülker, 1913).

III. Loliginidae with a distinct tooth[*] in the middle of the dorsal margin of the mantle (Figure 89); funnel adductors more or less distinct; fins transverse or longitudinal set, oval or rhomboidal, in adults occupying to three quarters of the mantle length. Subfamily Loligininae nov., with Loligo, Alloteuthis (see p. 207), Doryteuthis Naef, 1912, Lolliguncula Steenstr., 1881.

The determination of species is based on other characters which show certain norms and types that are subject to graded variations:

1. Coloration and distribution of chromatophores, especially the dark ones, which determine the typically recurring patterns. These patterns of coloration are more marked in the male than in the female and show distinct characters like spots on the fins and mantle, longitudinal stripes on the base of the fin and on the ventral midline of the mantle. These color characters must be used with care in systematics because they are individual and transient.

192 2. General proportions of the body: the length-width ratio of the mantle sac $({}^{2}/_{1}-{}^{8}/_{1})$; length ratio between arms and mantle sac. These also vary markedly according to the physiological condition, preservation, age, sex, race and locality, but these variations are not without systematic importance.

3. The length-width ratio of the gladius varies markedly with age, race and sex; it may also differ in local forms (my material consists almost solely of specimens from Naples), but it has to be used. More important are (p. 191) special characters of the gladius, e. g. a) the form of the anterior end (pointed, angular or rounded); b) the arrangement of the longitudinal ridges on the rhachis, the outline of the flag (lateral margins curved, parallel or extending straight posteriorly); c) the form of the posterior end of the gladius (distinct cone, remnant of rostrum; cf. Alloteuthis, Figure 72 on p. 171).

4. Dentition of the suckers, especially of the large suckers of the arms and tentacles. Number, arrangement and special form of the teeth; their partial reduction.

5. Relationships of size and arrangement of the suckers on the tentacle clubs (p. 177).

6. Form of the protective margins and their supports on the tentacle clubs (p. 178).

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[*] This tooth is evident also in the shell, which is produced here in a fine point, in contrast to the more parabolic end in the Septioteuthinae. This can be recognized from the growth lines also on a damaged gladius and permits the identification of isolated shells of Sepioteuthis which otherwise closely resemble those of Loligo.

7. Formation of the buccal points and the absence or presence of suckers on them (p. 178).

8. Form of external genital organs in the mantle cavity; presence of accessory glands in the male (cf. Loligo forbesi!).

9. Specific structure of hectocotylus.

10. Method of attachment of the spermatophores during copulation. This may vary even in one species (cf. Loligo vulgaris) and does not deserve the great emphasis given by Steenstrup (1881) when he established the genus Lolliguncula.

193 *Chapter 7*

GENUS LOLIGO

Lamarck, 1799

(**Sepia** L. pars)

Contents: a. Diagnosis. – b. Typical structure of the adult animal (p. 194). – c. Postembryonic development (p. 196).– d. Variation of the type of Loligo (p. 196). – e. Loligo vulgaris (p. 197).– f. Loligo forbesi (p. 202).

a. DIAGNOSIS

Fins of adults oblong-rhomboidal, occupying $^1/_2$ to $^3/_4$ of the side of the mantle. Buccal points with up to 15 small typical suckers in 2 rows. Posterior end blunt, not produced into a thin point or tail-like process. Mantle sac of adults moderately slender, 5–7 times as long as wide. Arms barely half as long as mantle.*

The generic name Loligo has been interpreted differently in the literature. Linné (1758, 1767) used it as the name of a species of Sepia (S. loligo). Lamarck (1799), used it for all Teuthoidea known at the time, together with the Sepioidea with a soft "gladius" (Loligo vulgaris, L. sagittata (Ommatostrephes and Illex), L. subulata (Alloteuthis subulata), L. sepiola (Sepiola, Rossia). D'Orbigny (1839) narrowed the concept. After removing the Oegopsida, and the genera Beloteuthis, Belemnosepia and Sepioteuthis, he applied the name Loligo to Loliginidae without any special characters (cf. p. 192). Vérany (1851) retained the name in general, but he considered a number of Oegopsida as species of Loligo.

Even after the restriction to the Loliginidae and after the removal of the above groups, the generic name remained a collective term for the family, of which several characteristic forms were later raised to genera.**

194 b. TYPICAL STRUCTURE OF THE ADULT ANIMAL

The typical habitus of an adult of the genus is shown in Figure 91 on p. 199 and Figure 92 on p. 200. Many descriptions of new species are based on juvenile specimens which show different characters that will not be considered here (cf. Figure 93 on p. 201).

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* This diagnosis is still more restricted than my previous diagnosis (1912). Note No. 4.

** Steenstrup established the genera Loliolus (1856) and Lolliguncula (1881). I separated L. plei Blainville 1823 as a genus, Doryteuthis (Naef, 1912, IV, p. 742).

The fins are oblong-rhomboidal and occupy about $^{1}/_{2}$–$^{3}/_{4}$ of the mantle length. Otherwise, the fins show the typical characters of the family (p. 172). The considerable length of the fins is associated with their function. The restless animals usually swim in a moderate, floating manner with undulating movements of the muscular plates without much action of the funnel or marked contractions of the mantle sac which performs regular, slow respiratory movements (p. 83). The wide fins undulate forward and backward with equal ease and in the same rhythm so that the animals swim forward and backward in a small aquarium, usually without turning. The funnel-mantle apparatus functions more actively only when the animal is in flight or in pursuit of prey.

The posterior end of the body is usually slightly rounded. In some preserved specimens of L. vulgaris, however, it is pointed where the fins meet as narrow ridges. This probably results from contraction of this part during preservation. At any rate, the usually rounded posterior end of the body is characteristic for typical specimens of Loligo and is caused by a secondary simplification of the gladius. The gladius of the adult Mediterranean Loligo does not have a distinct cone or a rostrum (as that shown in Figure 72 on p. 171); these structures have apparently been lost. Specimens with a complete gladius in which this could be observed are very rare, even if externally intact animals are examined (p. 171).

The mediodorsal toothlike process of the mantle margin resembles the corresponding structures in Alloteuthis, Doryteuthis and Lolliguncula. Loligo differs from Alloteuthis in the more parabolic outline of the process (Figure 89 on p. 190 and Figure 94 on p. 204).

The mantle sac is narrow, about 6 (5–7) times as long as wide.

(195)

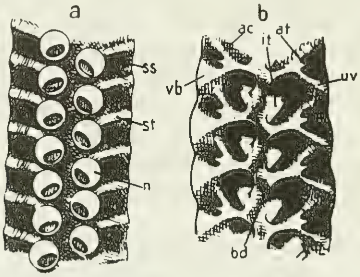

FIGURE 90. a) Inner surface of a dorsal arm, 2×; b) inner side of hand part of tentacle of a small Loligo vulgaris, natural size. The figure shows the relationships between the suckers and their supports and between the supports (st) of the protective margins (ss). In a) the suckers are preserved (n) and the relationships are normal (Figure 44 on p. 118). In b) the suckers are removed and fine rings show the position of their stalks on the conical supports. The large supports of the inner rows (it) are situated in pits (x), which are deepest before the supports and communicate with each other below the median ridge so that each pit is connected with the pits of two obliquely opposite suckers. As the pairs of suckers are situated close together in the middle, one of these connections is shorter than the other. The delicate supports of the marginal rows (at) are at first connected with the median axis of the arm by a large support which proves their primarily uniserial character (p. 116). From the base of this support extend two supports of the protective margin, one anterior (ac), the other posterior (vb, uv); the posterior support reaches the margin and the anterior ends before it. Note the widening of the supports on the ventral margin (vb).

The buccal funnel (Figures 77, 78 on p. 179 and Figure 79 on p. 180) shows the typical characters of the Metateuthoidea (p. 149); its points bear a variable number of distinctly biserial suckers. I observed up to 15 such suckers on the especially strongly developed lateroventral points.

The tentacle clubs show special characters. The suckers of the inner rows are situated in pits separated on the surface by a raised, bandlike median ridge. Between the pits is a zigzag-shaped longitudinal canal to which each pit has an access before the basal pad inside it (Figure 90b).*
195 This canal is formed during postembryonic development by fusion of the deep parts of the pits. The supports of the protective margins in the middle of the club are characteristic. The supports associated with the marginal suckers of the ventral row are widened into spatula-shaped structures toward the margin of the protective margin; the supports on the dorsal margin are normal (Figure 90 and Figure 94 on p. 204). From the supports of the marginal suckers (at) extends a distally directed accessory support which does not reach the margin (Figure 90, ac). As was explained on p. 178, these are displaced supports of the suckers of the inner rows (Figure 44 on p. 118; see also Alloteuthis, Abraliopsis, Ommatostrephidae, Sepiidae!).

The free margin of the suckers of the tentacle bears characteristic papillae or fringes, as in Lolliguncula (cf. also Sthenoteuthis). These structures vary greatly in form and size, particularly on the outer side; they are contractile in the living animal and are not uniform around the sucker but vary according to the space between the suckers. They are mainly distinct at the outer margin (sensory organs?).

In the mantle cavity the genital processes are displaced far toward the anus in both sexes (Figures 183 and 186), in contrast to Alloteuthis, in which they remain more or less in the gill base (Figures 98 and 99).

In the forms from Naples the developed hectocotylus bears a median row of 22–27 normal suckers (Figure 83 on p. 184).

Epigamic coloration. At least in the male (in Mediterranean species), short, narrow, flameshaped stripes of concentrated brownish-red chroma-
196 tophores appear at sexual maturity on the sides, and also a dark longitudinal line in the ventral midline of the mantle below the fins, along its base. The ventral median line of the mantle is connected with a thin, transient skin ridge (Figure 91 on p. 199). There are also a number of dark eye-spots on the dorsal side of the fins. All these markings almost disappear in preserved animals; the short spots on the mantle are most constant (Figure 91 on p. 199).

c. POSTEMBRYONIC DEVELOPMENT

Plates I and II give an idea of the major typical changes during postembryonic development. (Compare also Plates VI and VII of Vol. II and Figure 89 on p. 190 and Figure 93 on p. 201).

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* This character is typical for the whole family (cf. Sepioteuthis in d'Orbigny, 1839: Loligo, Plate V, Figure 15!). Its development is apparently inhibited in the smaller forms.

(199)

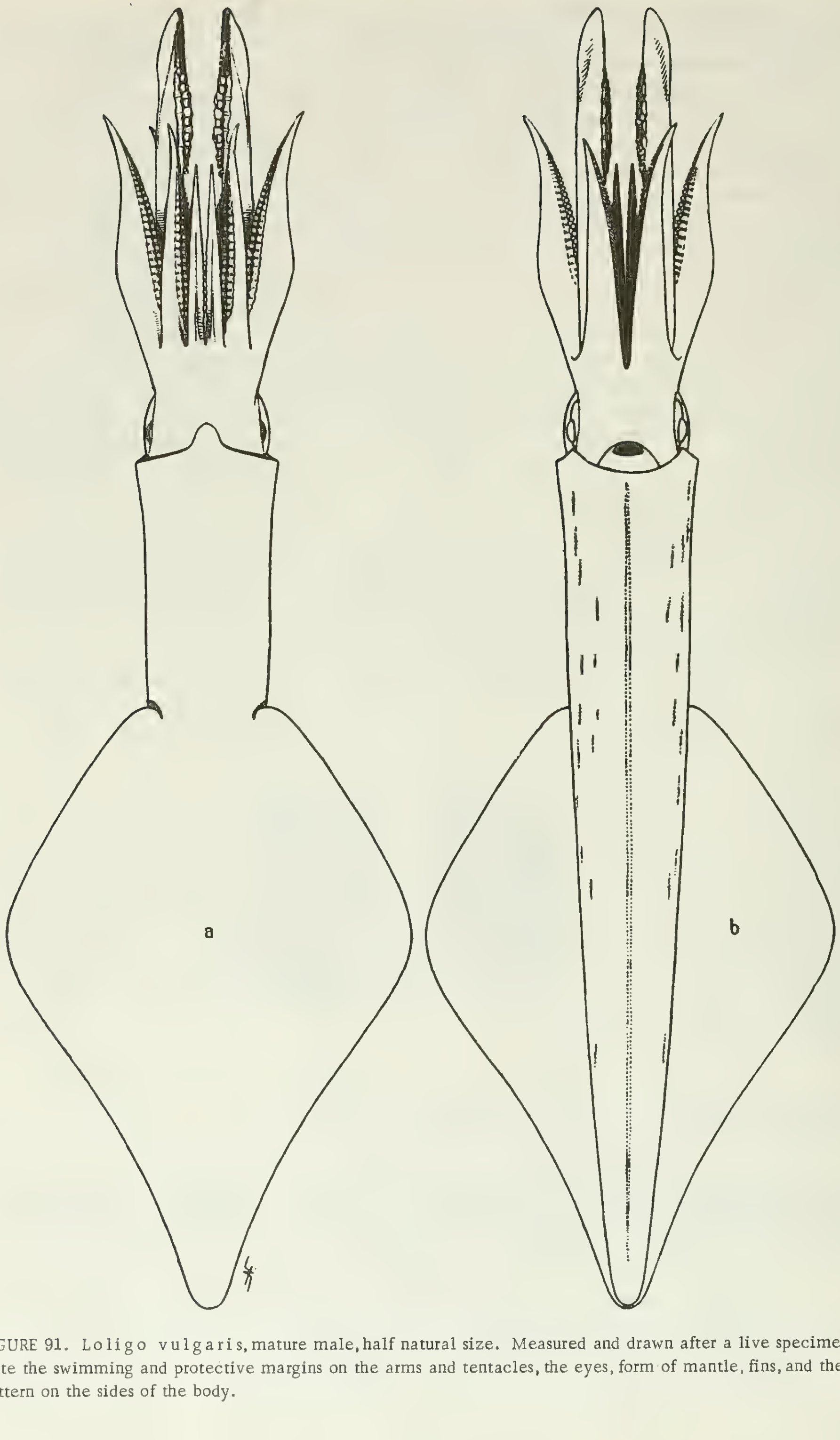

FIGURE 91. Loligo vulgaris, mature male, half natural size. Measured and drawn after a live specimen. Note the swimming and protective margins on the arms and tentacles, the eyes, form of mantle, fins, and the pattern on the sides of the body.

Most striking is the gradual change of the fins which become longer and are at first nearly circular (Plate I, Figure 3) but become later irregularly semicircular (Plate I, Figure 6). They form later a broad, transverse oval (Plate I, Figure 5) which passes into a rhomboidal-heart-shaped form (Plate II, Figures 4 and 5). This last form is at first wider than long and occupies only about half of the side of the mantle. It later becomes longer until it reaches its final form. Still later the fins become slightly pointed by an inflection of the posterior margin, while the anterior margin produces the "earlobes" (Figure 91, p. 199 and Figure 93, p. 201).

The mantle sac becomes increasingly slender. It is originally as long as wide (in the extended state), but it becomes gradually 2-, 3-, 4-, 5- to 7 times as long as wide. The dorsomedian toothlike process at the anterior margin becomes gradually more prominent (Plate I, Figures 3 and 5; Plate II, Figure 5).

d. VARIATION OF THE TYPE OF LOLIGO

The generic name Loligo includes also today all Loliginidae without any special characteristics and thus designates a diffuse group which is difficult to define. A thorough revision of the genus is urgently necessary, as Wülker (1913) did for the genus Sepioteuthis. Although a large number of species and forms can be identified from the literature, most descriptions are too incomplete for a scientific system to be based on them. The description of Loligo vulgaris shows that a useful characterization of the forms of the group has to include adult specimens of both sexes, not juvenile forms caught by accident. This merely causes confusion. I define the genus (p. 193) more strictly to contain only the species grouped around Loligo vulgaris as type, which form a natural group in the Loligo-like Loliginidae. Characters of forms not included here which, together with other characters, could be used for the establishment of new genera are the following:

197 1. Transverse-rhomboidal fins; 2. long arms, longer than half the mantle; 3. absence of suckers on the buccal points; 4. compact posterior body, less than 4 times as long as wide; 5. short-rhomboidal fins, occupying only a third to half of the side of the mantle; 6. short, transverse-elliptical fins, as in Lolliguncula Strp., 1881; 7. ending of the wide surface of the fins several centimeters before the posterior end, without forming a tail-like process as in Alloteuthis (Figure 101); end of body instead spindle-shaped, accompanied by mere ridges of fins (Munich Zoological Collection).

Some of these characters are persistent juvenile characters, but they may also occur in the adults (3, 4, 5, 6). They are mentioned here only as indications for further systematic work.

e. LOLIGO VULGARIS Lamarck, 1799

DIAGNOSIS

Fins of adult occupying over two thirds of sides of the mantle. Suckers of tentacle clubs 3–4 times larger in the median rows than in the lateral rows and often without teeth, at least at the lower margin. Male with short, longitudinal stripes of dark, concentrated chromatophores on the sides of the mantle.

LITERATURE

This species is known from antiquity in the Mediterranean. It appears in Aristotle (IV., I) under the name Teuthos, in Pliny (lib. IV., cap. XIX) as Loligo. Other authors have described it under the following names:
1551 Belon (lib. II., p. 340) as Loligo.
1554 Rondelet (lib. XVII, pp. 506–510) Loligo magna.
1642 Aldrovandi (pp. 67–71) L. major.
1758 Linné (1767, p. 3150) Sepia loligo.
1799 Lamarck (t. I, p. 11) L. vulgaris.
1817 Cuvier (Vol. 2, p. 9) S. loligo.
1822 Lamarck (p. 366, 12th ed. 1845) L. vulgaris.
1823 Blainville (t. XXVII, pp. 143–144) L. vulgaris + L. pulchra (juv.).
1823 Férussac (t. III, p. 67) L. vulgaris.
as well as: Carus, 1824; d'Orbigny, 1826; Risso, 1826; Payraudeau, 1826; Delle Chiaje, 1827; Wagner, 1828.
1839 Férussac and d'Orbigny (p. 308, Plates 8, 10, 22, 23) – L. vulgaris. Specimens of L. forbesi are also included (Plate 8, Figures 1 and 2). Also in the following work (p. 93).
1851 Vérany (p. 89, Plate 34) – L. vulgaris. Here belongs also a juvenile specimen (Plate 36, Figures h, i, k) which is named L. berthelotii.
1845, 55 d'Orbigny – L. vulgaris, also Steenstrup (1856).
1858 Adams L. magna (forbesi?) and L. neglecta.
1869 Targioni-Tozzetti L. vulgaris, L. mediterranea (contains the very large specimens), L. berthelotii Vér.
1869 and 1872 Fischer L. vulgaris, L. pulchra Blainv. (juv.), L. berthelotii Vér. (juv.), L. affinis Laf. (juv.), L. microcephala Laf. (juv.).
1869 Jeffreys (p. 130) L. vulgaris.
1871 Woodward (p. 167) L. vulgaris.
1879 Tryon (p. 145) L. vulgaris.
1880 Tiberi (pp. 20, 21) L. vulgaris and L. berthelotii Vér.
1880 Stossich (p. 159) L. vulgaris.
1885 Ninni (p. 159).
1886 Hoyle (p. 34 (L. vulgaris = (L. pulchra Bl., rangii Fér., neglecta Gray, berthelotii Vér., mediterranea Targ., pulchra Fischer).
1890 Norman (p. 480) L. vulgaris.
1890 Girard (p. 253) L. vulgaris.
1890 Kolombatovic (p. 12) L. vulgaris.
1890 Carus (p. 456) L. vulgaris and berthelotii Vér. (doubtful).
1894 Pelseneer (p. 205) L. vulgaris.
1896 Jatta (p. 167, Plates 3, 8, 17) L. vulgaris.
1908 Pfeffer (p. 27) L. vulgaris.
1916 Naef (p. 14) L. vulgaris (System).
1921 Naef (p. 537) L. vulgaris (System).
1921 Grimpe (p. 299) L. vulgaris (North Sea).

The habitus is shown in Figures 91 on p. 199 and 92 on p. 200. These should be compared with Figures 4 and 5 of Plate II which show juvenile proportions but otherwise do not differ markedly from the definitive habitus. A good color drawing (by Merculiano) is given by Jatta (1896, Plate III, Figure 4).

The gladius* (Figure 69 on p. 169) shows the typical conditions of the genus, and except for the simplified end, of the whole family (Figure 171). Its proportions vary markedly according to sex, age and variety. The length/width ratio of adult specimens is 5.4 (female) to 8.2 (male), average about 6.8 (cf. p. 200). The corresponding ratio of the mantle sac varies correspondingly, with an average of about 6.

The structure of the tentacle club is characteristic for L. vulgaris; it differs markedly from that of the otherwise similar L. forbesi, in which all 4 rows have suckers of about equal size. The suckers of L. vulgaris differ markedly; those of the median rows of the hand part are about 3–4 times as large as the suckers of the marginal rows (Figure 92 on p. 200 and Figure 94 on p. 204). There are 3–5 large suckers in each median row. These differences disappear in the distal part, where the ventral row consists of slightly larger suckers. The dentition of the horny rings on the large suckers shows irregular gaps. The teeth at the lower proximal margin are often absent, but they may also be incomplete on the other sides of the ring. I could not establish varieties, local forms or subspecies on the basis of dentition, but I believe that they exist.

The structure of the normal suckers of the arms is shown in Figure 75 on p. 176 and Figure 1 of Plate XII.

The proportions of the body of the species vary widely and cannot be defined numerically. They apparently have a wide range, although there are distinct regularities, and the vagueness is caused and increased by the fact that the differences between the two sexes appear only at the approach of sexual maturity. In general, marked changes take place during postembryonic development (p. 193); moreover, as maturity begins at very different sizes, which becomes evident during comparison of the sexes and of specimens of the same size, the picture is confused. To establish varieties or local forms, populations have to be examined at a certain time
199 and place; I did not realize this early enough, and buying material on the fish market would have been rather expensive.

200 Sexual differences. The proportions of the body of the two sexes vary markedly. A mature female** with a mantle length of 18–29 cm has a mantle sac 5 times as long as wide. Adult males are larger and I found a ratio of about 6 for specimens with a mantle length of 18–35 cm. The males become slenderer at maturity, the females stouter; juveniles of both

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* Compare also the figure on p. 28 in Jatta, 1896, as well as Figure 3 of Plate 32 in Quenstedt, 1849, in which the inner asymptotes are distinct as in Figure 62, p. 146. Because of its importance for the comparison between fossil and recent gladii, this character should not be overlooked, although it is a minor character. The stripes are formed only by a small inflection of the growth lines which delimit the cone parts of the flag and are often thicker and more intensively colored.

** In well-preserved specimens, which resemble the proportions of the live, resting animals (p. 194); the width of the mantle was measured in the middle between the anterior margin of the base of the fin and the margin (cf. Plate I and II).

sexes are rather uniform, with a ratio of 2–4. The state of contraction of
the mantle is important, and exact measurements are pointless. Better
201 results are obtained from measurements of the gladius, the length/width
ratio* of which changes corresponding to that of the mantle sac. The form
of the gladius depends on that of the mantle sac, although it is difficult to
decide which of the two is the causative factor. However, I believe, that the
gladius follows the widening of the mantle sac and not vice versa, if the
marginal growth is measured correspondingly.

(200)

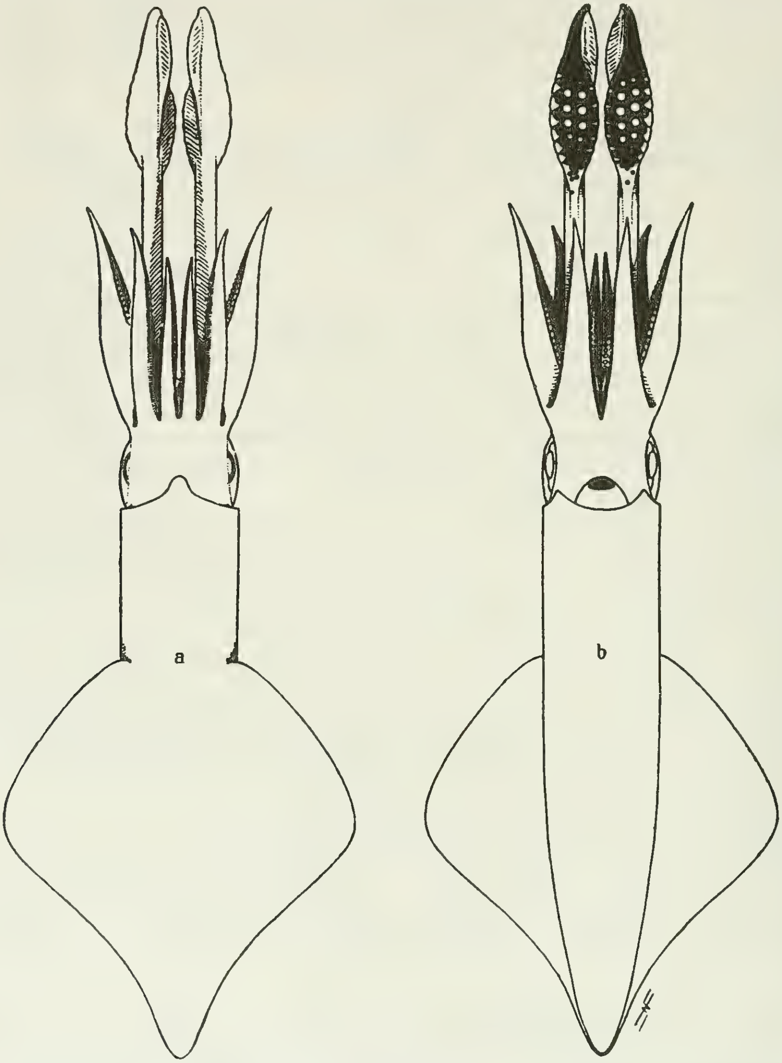

FIGURE 92. Loligo vulgaris, mature female, half natural size. Compare with Figure 91 with respect to the outline and proportions of the mantle and the proportions of the head and arm apparatus. Note the attachment of the buccal funnel and the form of the tentacle clubs. Figures 84, 85 on p. 185 and Figure 69 on p. 169 show the same specimen after further preparation.

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* The width was measured as follows: the lateral margins are pressed at the widest place on a plane surface to eliminate the curvature of the flag but not of the keel (Figure 71 on p. 170).

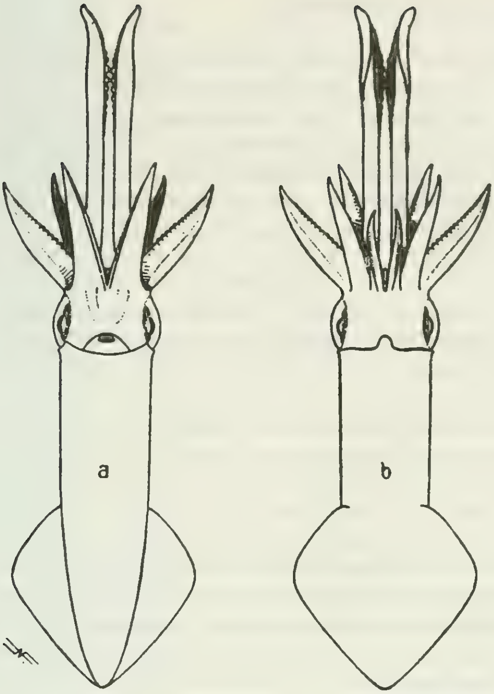

FIGURE 93. Loligo vulgaris. The young specimen shown in Plate 2, natural size. Drawn after a nearly dead animal, all proportions being exactly measured. The tentacles are shown in their natural position, but not in contact as in the live animal (cf. p. 158). The arms have been spread. Note particularly the position of the swimming margins on the clubs, the curvature of the cornea, the orbital pore, the eyeball and iris flap (b), the pupil and lens (black), the form of the mantle margin and the outline of the fins.

The length/width ratio of the gladius of mature males with a dorsal mantle length of 18–35 cm varies from 7 to 8.2, that of mature females of 18–29 cm length from 6–5.4. Large, fully mature specimens show the extreme values. However, there is no strict regularity, since sexual maturity does not always appear at the same size. I found females only 12 cm long, but already mature and mated. I did not find mature males less than 20 cm long. On the other hand, I hear from creditable sources that specimens of 1 m length or more (without tentacles) have been found. The large male shown in Figure 91 on p. 199 is not completely mature.

The epigamic coloration of the male shows some characters which are never found in females. Several reddish brown transient eye-spots appear on the fins, while dark longitudinal lines appear along the fin base. The ventral midline of the mantle forms a thin, dark skin fold, and the sides of the mantle show several short longitudinal stripes which are similar, but much smaller and less intensely colored than in L. forbesi.

202 Before the modified end of the hectocotylus of the male L. vulgaris, the median row bears 25–27 normal suckers, not counting the first sucker, even if it apparently belongs to the median row. There is a larger number of normal suckers in young specimens, so that a successive conversion of typical into atypical suckers, beginning at the apex, has to be assumed.

POSTEMBRYONIC DEVELOPMENT

Plates I and II show a series of postembryonic stages resembling those in Figures 91–93. A number of special characters are added here to the data on the family and genus. The mantle sac becomes longer and slenderer, about 4 times as long as wide (Figure 93 on p. 201), but this lags later in the female (p. 200) and specimens with fully developed genitalia have a slightly wider mantle sac. On the other hand, the gladius becomes at first slenderer and then again gradually wider. Thus, at a mantle length of 4.2 cm I found the ratio 6.6; at 8 cm, 6.3; at 12 cm, 6. The two sexes later become more different.

The eggs vary markedly in size. Their length (without membrane) is 2–4 mm. Similar differences were found among the juvenile stages.*

f. LOLIGO FORBESI Steenstrup, 1856

DIAGNOSIS

Fins extending on about three quarters of the side of the mantle in adults. Suckers in median row of tentacle club not markedly larger than those of the marginal rows, with more or less regular dentition all around. One rudimentary accessory nidamental gland present also in the male. Sides of mantle with scattered longitudinal stripes with concentrations of dark chromatophores in both sexes.

LITERATURE

Because of the incomplete early information, it is difficult to determine whether the authors had this species in addition to L. vulgaris. This is probably the case, for example, in Boussuet (1558, p. 200, "L. magna") and Borlase (1750, p.266, Plate 25, Figure 32, "L. biscala").

1839 Férussac and d'Orbigny. Specimens of L. forbesi are shown as L. vulgaris in Plate 8, Figures 1–2.
1851 Vérany (p. 93). A variety of L. vulgaris with more uniform suckers on the tentacle clubs.
1853 Forbes and Stanley (Vol.4, p.226) L. vulgaris.
1856 Steenstrup. The first definite identification of L. forbesi.
1858 Adams (Vol. 5, p. 37) L. magna Rond.
203 1869 Targioni-Tozzetti (p. 33, Plate 7, Figure 10) L. forbesii Strp.
1869 Jeffreys (Vol. 4, pp. 130–131) L. vulgaris (The author believes that his specimen of L. forbesi is a female of L. vulgaris).
1870 Lafont, L. forbesii and L. moulinsii Laf.
1871 Lenz (p. 135) L. forbesii.
1872 Fischer (p. 19) L. forbesii (in addition L. moulinsii Laf.).
1879 Tryon (p. 147, Plate 56, p. 178) L. forbesii.
1884 Giard (p. 306) L. forbesii.
1886 Hoyle (p. 35) L. forbesii, in addition L. magna Rond.
1890 Norman (p. 480) L. forbesii.

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* I observed in the different eggs of Sepia and Sepiola, that the mutlicellular embryos obtained from the largest eggs are more suitable for morphological studies because such rudimentary structures as the primary connection between kidneys and pericardium is clearly visible in such eggs, while in the small normal eggs of small littoral specimens this is hardly visible. The large eggs are from deeper water, at least in the Bay of Naples. The larger animals are also more complete morphologically. For example, the number of suckers on the buccal membrane is larger (to 15 on the third point, usually only 10–12).

1890 Girard (p. 254) L. forbesii.
1890 Carus (p. 455) L. forbesii.
1894 Joubin (p. 6) L. forbesii.
1896 Jatta (p. 174, Plate 8, 30) L. forbesii.
1908 Pfeffer (p. 27) L. forbesii.
1912 Wülker (p. 201, Plate 24) L. forbesii.
1916 Naef (p. 14) L. forbesii.
1921 Naef (p. 237) L. forbesii.
1921 Grimpe (p. 299) L. forbesii.

DESCRIPTION OF THE ADULT ANIMAL

This species is common in the North Sea; it is much less common than L. vulgaris in the Mediterranean. There are usually only a few large specimens, mainly immature males on the fish market in Naples.

This species is easily recognized by the suckers on the tentacle club (p. 204), and by the narrow, spindle-shaped, flamelike longitudinal lines on both sides of the mantle. These lines are present in both sexes and are much larger and more intensively colored than in males of L. vulgaris (Figure 92 on p. 200; cf. Jatta, Plate 30, Figures 1–16, Plate 8, Figure 5, which is an accurate colored drawing showing the difference in tone from L. vulgaris which is more pink. However, the real differences are not as marked as may be assumed from the drawing, which apparently was not made from a live specimen).

The different habitus of L. forbesi and L. vulgaris is evident even to the moderately experienced observer. Fishermen never confuse the two species. L. forbesi is called "Occhione" in Naples because of its large eyes; Figure 94 on p. 204 shows clearly that the compact form of the animal is also expressed in the markedly thicker head.* The figure was drawn from a preserved specimen, except the outline of the mantle, and a strict comparison of its proportions with those shown in Figure 91 on p. 199 and Figure 92 on p. 200 is therefore not possible. Moreover, the specimen shown here was not quite mature. The mature male is much slenderer, the width of the mantle at least 6 times its length on the dorsum. Loligo forbesi is at least as large as L. vulgaris (p. 201), probably much larger, and it shows a similar variation in the sexes and stages of maturity. The width of the gladius probably also varies similarly (p. 201). In large specimens, the fins occupy about three quarters of the side of the
204 mantle, that is, more than in L. vulgaris. The arm apparatus and buccal funnel resemble those in L. vulgaris. The tentacle club, however, differs sharply from that of L. vulgaris. The suckers of the hand part are also enlarged, but far less than in L. vulgaris, but the suckers of the median rows are only slightly larger than those of the marginal rows; closer
205 examination shows that there is a marked difference (Figure 94). The suckers are toothed regularly all around, although there may be gaps between the teeth.

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* This is partly because the specimens have a more juvenile habitus than specimens of L. vulgaris of the same size. Compare Figure 93 on p. 201 with Figure 94 on p. 204! Mature animals certainly have about the same proportions as L. vulgaris as proved by the largest males examined (about 80 cm). I have not seen fully mature specimens.

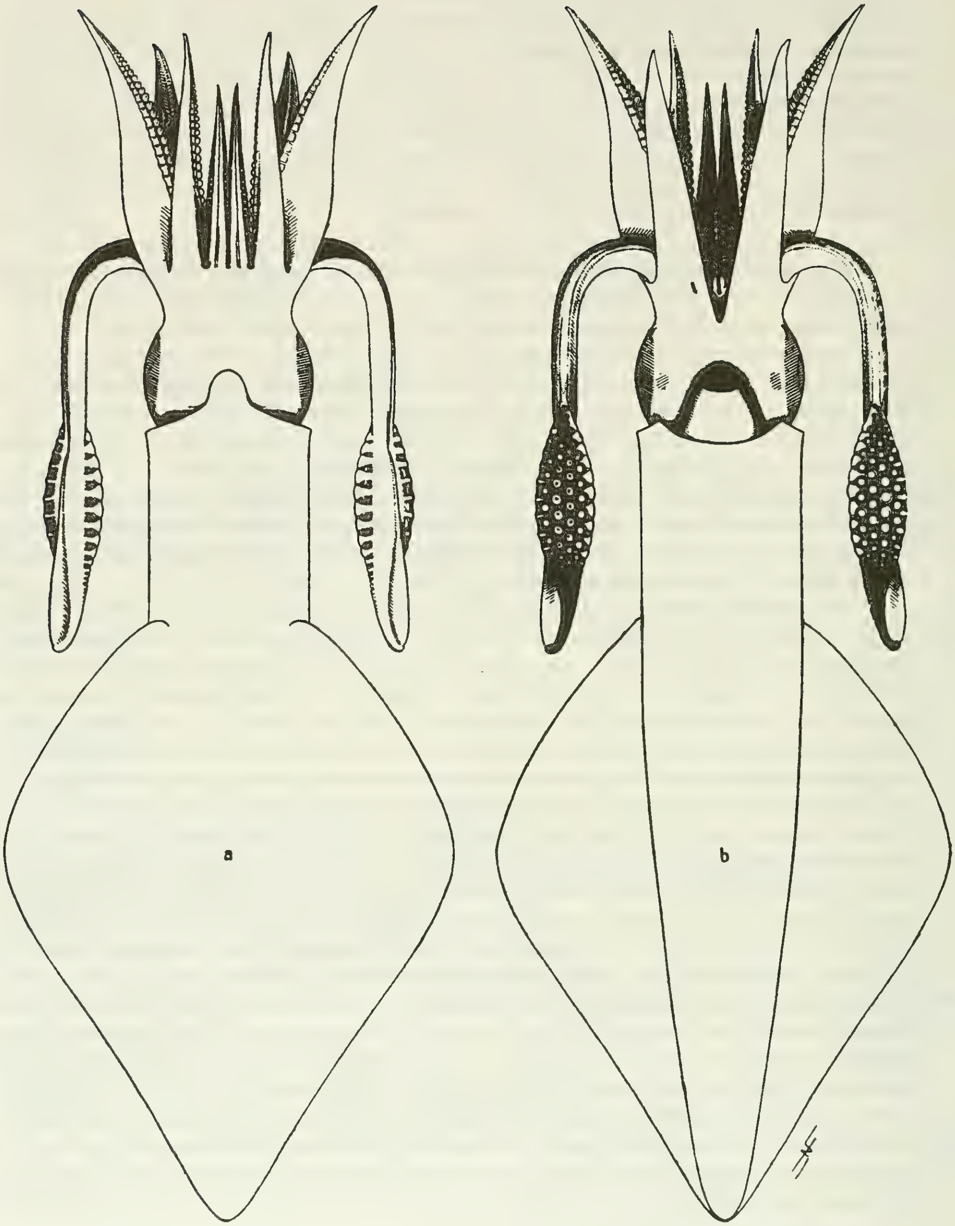

FIGURE 94. Loligo forbesi, young male. Half natural size. Compare the proportions with Figure 91 on p. 199. Note particularly the structure of the tentacle clubs.

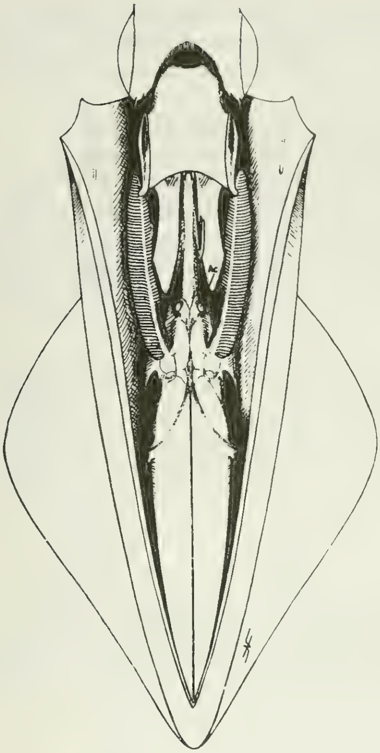

FIGURE 95. *Loligo forbesi*. Same specimen as in Figure 94, after opening of the mantle. The attachment of the soft body to the shell is clearly shown. Note the small accessory glands (Ac) of the male, which are shown as white spots before the renal papillae; neck folds, funnel pits and funnel bonds, of which also the anterior half is cartilaginous and appears darker. The figure is drawn from the same specimen as in Figure 94.

The mantle cavity also shows much the same relationships as in *L. vulgaris* in both sexes. There is, however, one important character: also the male has accessory nidamental glands, but these grow more slowly than in the female and never develop completely. In larger specimens the accessory nidamental glands form two low pads on the ink sac, on each side of the renal papillae (Figure 95, Ac). The detailed structure of these glands, which resembles that of a normal accessory gland, was described by Wülker (1912), who discovered them independently and studied them in detail. This is apparently a case of the common hereditary transfer of a character to the other sex. This is of particular ecological interest, but it has no connection with primary or secondary hermaphroditism. It may be explained by assuming (cf. p. 126) that the accessory nidamental glands have other
206 functions in addition to those associated with egg deposition. They may secrete, at least temporarily, luminous substances, which results in differentiations in the Sepiolidae (cf. Naef, 1912, Note 7; also 1916). Many Oegopsida have luminous organs at the same point (see Plate IV, Figure 3; also *Octopodoteuthis*, Figure 166).

Because of scarcity of material, particularly of larger females, I could not make a detailed study of sexual dimorphism in this species. It probably has the same characteristics as in *L. vulgaris* (p. 201). The end of the hectocotylus shows the changes typical for the family (Figure 83 on p. 184). In half-grown specimens examined I found that the median row still has 22—26 normal suckers; the latter figure is more common. (The first sucker of the arm always belongs to the lateral row and should not be counted, even if it appears otherwise.)

Juvenile specimens of L. forbesi closely resemble those of L. vulgaris. Differences become evident only at a certain size (approximately as in Figure 68 on p. 169), the median suckers of the club become larger in L. vulgaris but are almost of the same size as the others in L. forbesi. However, I am not certain that my young specimens are actually L. forbesi. In general, what was said on p. 202 also applies here.

207 *Chapter 8*

GENUS ALLOTEUTHIS

(Naef, MS.) Wülker, 1920

(= **Teuthis** Aristoteles, Schneider, 1784)

Contents: a. Diagnosis. – b. Literature. – c. Typical structure of the adult animal (p. 209). – d. Juvenile forms (p. 212). – e. Variation of the type of Alloteuthis (p. 213). – f. Alloteuthis media (p. 215). – g. Alloteuthis subulata (p. 219).

a. DIAGNOSIS

Points of buccal funnel short, indistinct, without suckers. Posterior end of mantle produced into a thin point or a tail-like appendage. Fins forming together a heart-shaped figure. A long genital process absent in the female, but present in the male near the gill base.

b. LITERATURE

A strict distinction of the species did not exist before my studies (1912, Note No. 5, p. 745). The specimens described by other authors were therefore probably a mixture of the European species, except when they had a homogeneous material. Even when they thought they could distinguish between the European species, they lacked sufficient knowledge. The literature therefore applies only to the genus, not the species (but see pp. 216 and 219).

1554 Rondelet (lib. XVII, p. 508). The figure certainly represents Alloteuthis media, of my determination (see p. 216) – Loligo parva.
1758 Linné (ed. 1767, pars VI, p. 3150). The species of Rondelet named Sepia media.
1784 Schneider (p. 112) Teuthis.
1789 Bruguière tab. LXXVI, Fig. 9 Sepia media.
1799 Lamarck (12. edit., 1849, Vol. II, p. 368) Loligo subulata Lam. (Atlantic?).
1802 Bose (tom. I, p. 46) Sepia subulata Lam.
1805 Montfort (tom. II, pp. 74, 82) Sepia subulata Lam.
1816 Cuvier (3. edit. 1836, Vol. 2, p. 9) Le petit Calmar (S. media Lam.).
1817 Leach (tom. III, p. 138) L. parva.
1823 Férussac (tom. III, p. 67, No. 6) L. spiralis Fér.
1823–27 Blainville (Vol. XXVII, p. 143) L. subulata Lam.
1826 D'Orbigny (p. 153) L. subulata.
1826 Layraudeau (p. 172, Nr. 350) L. subulata Lam.
1831 Delle Chiaje (tom. IV, pp. 48, 58) L. subulata Lam.

1836 Philippi (p. 202) L. subulata Lam.
1837 Verany (p. 91, Plate 5) L. marmorae = S. media L. () L. subulata Lam. Also 1840: both species are illustrated!
1838 Potièz and Michaud (tom. I, p. 8, Nr. 2) L. subulata Lam.
1839 Férussac and D'Orbigny (p. 310, Plates XVII, XXXIII, Figures 19, 21). (1848) L. parva Rond. = S. media L. female = L. marmorae Vérany.
1841 Cantraine (p. 17) L. subulata Lam.
1844 Philippi (b, p. 203) L. marmorae Vér.
1844 Thompson (p. 248) L. subulata Lam. (+ L. media Lin.).
1848 Requien (p. 619) L. subulata Lam.
1849 Gray (e, p. 76) Teuthis parva Rond.
1851 Vérany (c, p. 95) L. marmorae Vér. (Considers S. media and subulata as belonging to L. marmorae. Illustrations of both species (see below)).
1853 Forbes and Stanley (Vol. IV, p. 230) L. media Lin. = L. subulata Lam. et auct.
1855 (1845) D'Orbigny (p. 339) L. parva Rond. = L. media Lin. = L. marmorae female Vér. (!).
1856 Steenstrup (p. 220) L. subulata Lam. differs from L. marmorae (L. media Lin. is considered as identical with L. subulata Lam.).
1858 Adams, H. and A., (Vol.I, p. 38) Teuthis parva Rond. (Gray).
1869 Jeffreys (Vol. V, p. 132) L. media Lin. (L. marmorae is considered as its female, compare d"Orb. 1855).
1869 Targioni-Tozzetti (pp. 40–41) L. marmorae Vér. = L. subulata Lam., S. media Lin., L. parva Rond.
1879 Tryon (p. 149) L. media Lin. = L. marmorae Vér.
1880 Tiberi (p. 21) L. subulata Lam.
1885 Ninni (p. 159) L. marmorae Vér.
1886 Hoyle (p. 30) L. media Lin. (= L. subulata Lam. + L. spiralis Fér. + L. parva (Rond.) d'Orb. + L. marmorae Vér. (?).
1886 Hoyle (Notes, p. 279) L. media Lin. = L. marmorae Vér.
1889 Posselt (a, p. 243) L. media Lin.
1890 Norman (p. 481) L. marmorae Vér. well distinguished from L. media L.
1890 Girard (b, p. 254–257 c, p. 34–35) Teuthis media L. = T. marmorae Vér. Ibid. 1892.
1890 Carus (p. 456) L. marmorae Vér. differs from L. media L.
1893 Joubin (c, p. 1) L. media Lin. = L. subulata Lam. (?).
1896 Jatta (p. 183–188, Fig.) L. marmorae Vér. and L. media L.
1907 Massy L. media L. considered different from L. marmorae Vér.
1908 Pfeffer (same).
1912 Naef (p. 748) Teuthis Gray.
(see below, p. 209).

Schneider (1784) recognized that these species belong to a different type which deserved generic rank and proposed the name Teuthis. Aristotle used the name Teuthis for the smaller of the two species of Loligo known to him (the larger is Teuthos).*

Linné unfortunately named a fish Teuthis (1766), so that Schneider came too late according to rules of nomenclature. Many authors have nevertheless accepted his name (Gray, 1849; Adams, 1858; Girard, 1890). D'Orbigny (1845) and Vérany (1851) chose not to use the name because of

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* There is great confusion about the species of Aristotle (cf. Aubert, 1862, Keller, 1913). If it is considered that these are the common species found today on all Mediterranean markets, it is clear that Aristotle knew 6 Octopoda (**πολυποδες**), including probably the Sepiolidae, and 3 Decapoda: **σηπια**, **τευθις** and **τευθος** i.e. Sepia officinalis, Loligo vulgaris and Alloteuthis media. This agrees also with the description:
Teuthis is more pointed, with relatively wider fins, which are more restricted to the posterior end.
Teuthos is much larger, more blunt, with narrower fins which are longer and surround the posterior end.
Compare Figure 91 on p. 199 and Figures 96, 97 on p. 210.

the uncertainty and difficulty of the definition of the genus and species and
209 most authors accepted this. Only in 1912 was I able to establish the characteristics of the different species on the basis of a large material and gave a preliminary definition of the generic characters. I again proposed the name Teuthis, which seems justified. Berry (1913, p. 590), proceeding from the artificial priority of Linné, proposed the name Acroteuthis, which I accepted reluctantly and wrongly (Naef, 1916, p. 14). In fact, Acroteuthis was already preoccupied by Stolley for a belemnite (Geol. Pal. Abh., p. 219). I used the name Alloteuthis already in 1916 in manuscript and reprints from which the name was taken by Wülker, who adopted it (1920, May, p. 56) as a synonym of "Loligo" media L., which established its nomenclatorial validity* (cf. Naef, 1921, System, p. 539).

c. TYPICAL STRUCTURE OF THE ADULT ANIMAL

The general habitus of the genus is determined by the form of the posterior end, which differs more or less sharply from that of other Loliginidae. The posterior end is produced into a thin, distinct point or tail-like appendage (cf. Oegopsida, Chapter 9) which varies widely in form and changes during preservation (Figures 96, 97 on p. 210). Young animals always have a simple point (Figure 68 on p. 169), which is the primary form of all Loliginidae. The apex later becomes more or less longer, more distinctly in the male. The resulting caudal appendage is in a large part a process of the mantle sac in which even the mantle cavity continues; however, it contains at the end the rudimentary cone with the small rostrum (Figure 72 on p. 171) which supports the extreme end. This end of the gladius is a primitive character of the Teuthoidea which also occurs in other Loliginidae (Loligo pealei, for example) but it is better preserved in some Oegopsida.

The form of the fins is mainly influenced by the pointed posterior end. They are heart-shaped, especially in the early stages (Figure 68 on p. 169 and Figure 89 on p. 190). The apex of the fin becomes increasingly produced to the same extent as the end of the body grows (Figure 94 on p. 104). In all large specimens, however, the fins resemble the more rhomboidal form of Loligo (Figure 92 on p. 200), in which the blunt lateral corner is distinct.

The mediodorsal process of the mantle margin has a characteristic form. It forms not a parabolic curve as in Loligo (Figure 94 on p. 204) but a square with slightly rounded corners (Figure 97 on p. 210). This is not always distinct (slightly less so in A. subulata than in A. media); it may also be obliterated by bad preservation. In any case, this process, which contains the anterior end of the gladius, is more sharply distinguished from the rest of the mantle margin in Alloteuthis than in Loligo.

210 The characteristic point of the gladius is only distinct in good preparations. Otherwise, the general form of the gladius resembles that of Loligo. Similar variations due to sexual dimorphism are also found here, but I cannot give definitive data because of the wide variations in each sex and species in connection with the general variability.

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* Berry still used the name of Acroteuthis in March, 1920 (p. 56); informed by Wülker, he created the name Acruroteuthis (October, 1920). Grimpe (1921, Syst. p. 302) invented the name Acrololigo. I hope that this is the end of this "cooperation."

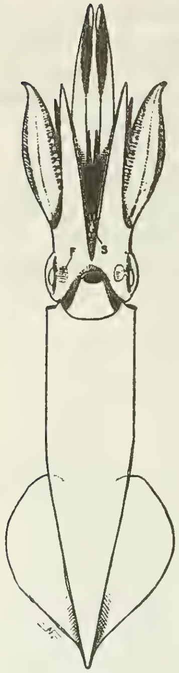

FIGURE 96. Mature female of Alloteuthis media, natural size, showing the typical habitus of the genus. Measured and drawn from a live specimen. Note the posterior end, fins, swimming and protective margins on the arms, buccal funnel with a round white spot (translucent spermatophore pad, S) — obviously a mated animal. F — window of outer wall of eye chamber.

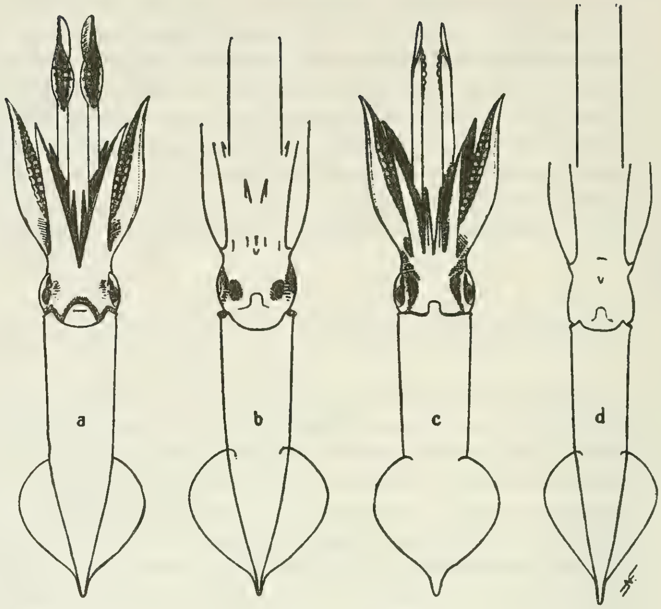

FIGURE 97. Two mature males of Alloteuthis media. a) and c) — ventral and dorsal view of a specimen measured and drawn alive and prepared and drawn again in the exact proportions in b) to show the changes. Note particularly the tail, the mantle margin (its mediodorsal part dotted), the outline of the head, and the short arms. The natural relationships can be reconstructed from Figures 101 on p.217, 102 on p.218 and 103 on p.220 with the help of this drawing. d) Preserved, particularly slender specimen, perhaps a variety. All drawings natural size.

The absence of suckers on the points of the buccal funnel is characteristic. In preserved animals, it is difficult even to recognize the points
211 as the funnel usually appears as a thick, swollen membrane, the inner side of which is folded as in Loligo and without differentiations. The short points and supports are clearly visible in a live animal and also in good preparations (Figure 76 on p. 177).

The tentacles and their clubs show the general pattern of the Loliginidae (p. 117). The typical hollowing of the hand part, however, is suppressed (Figure 90). The large suckers are situated in shallow pits. The suckers of the dorsal inner row are always distinctly larger than those of the ventral row (Figures 101 and 102). They are finely toothed all around, but not quite regularly: between the larger teeth are smaller teeth, often regularly alternating.

The supports of the protective margins of the club differ from the typical condition. The accessory supports situated distally to the suckers of the marginal rows (p. 195) also reach the margin, so that the margins have twice as many supports as marginal suckers (Figure 101). This is apparently a reversion to primitive conditions (Figure 44 on p. 118). When the suckers were not yet definitively arranged in 4 rows, this condition was probably normal (cf. similar patterns in the Ommatostrephidae, and in Abraliopsis, p. 292, on the normal arms).

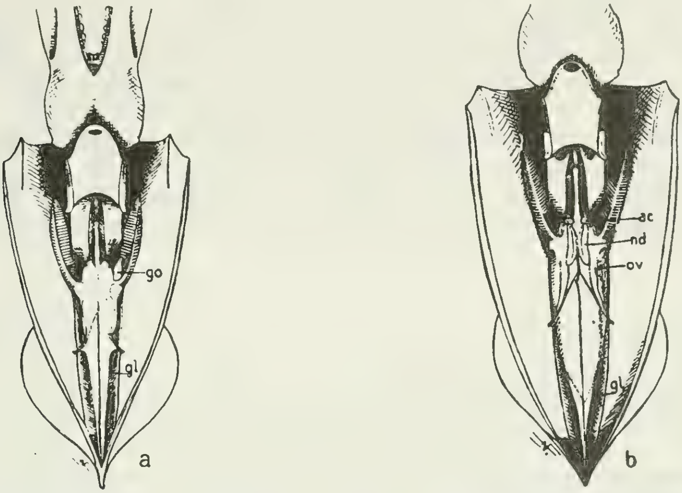

FIGURE 98. Situs of mantle cavity of Alloteuthis media, natural size. a) Mature male. Note the characteristic genital papilla (Go) in the left branchial corner, which projects markedly; other characters as in the Loliginidae. b) Young female. Comparison with Figures 81 and 82 shows the essential similarity. However, the form of the nidamental (nd) and accessory (ac) glands is different. The genital papilla is situated entirely in the pocket of the base of the gills; the oviduct (ov) behind the papilla shows already the typical curvatures. gl — margin of gladius.

The supports situated before the marginal suckers of the ventral row are indistinctly widened into spatula-like structures and only on part of the club. This is distinctly visible only in well preserved specimens.

The funnel supports resemble in form those of Loligo, but the curvature outward of the posterior end is smaller (Figures 94 and 99).

There is a marked difference from Loligo in the entire mantle cavity, although the essential characters are similar. The gills are shorter and situated more anteriorly, the hind intestine projects from the body, and its only connection with the anal papilla is a skin fold. This results in a more
212 strict symmetry in the formation of the inner organs (vena cava, venous branches, ink sac), giving them more space and corresponds to the primary condition of the younger stages of Loliginidae. The variations of the genital organs from the type are particularly distinct: the genital papilla of the male grows, as always, directly from the gill base and remains attached to the body for a short distance toward the median side (Figure 98).

Further growth toward the anus which takes place in Loligo does not occur in this species, so that the genital organ is apparently situated directly on the gill base. The genital opening of the female (Figure 99) is situated in the pocket of gill, and a genital process is absent. The nidamental glands of the adult also differ markedly from those of Loligo (cf. Figures 84 and 85). They diverge in their greater part, not including the median pallial artery closely, and extend only a little posteriorly near the artery. The (superficial) course of the oviduct is also very different (Figure 99).

The genital arm of the male is typical. In adults the median row has 9–16 normal suckers; there are usually 11 in A. media and 15 suckers in A. subulata. Strangely, the northern form of A. subulata resembles A. media more closely than the Mediterranean form in this respect.

In the males the suckers of the arms are distinctly but not markedly larger than those of the female. The arms of the male are also relatively stronger, but the tentacles are markedly slenderer than those of a female of the same size. In general the males are more slender and delicate. Compared with a female with a similarly large head, the male has a smaller posterior body (excluding the tail) and a longer tail appendage.

d. JUVENILE FORMS

The newly hatched animals resemble those of Loligo (Figure 88), except for the number of suckers on the club etc., which at any rate is not constant (cf. p. 189). The following stages are also very similar, to the conditions shown in Figure 89 on p. 190, in which a number of generic (but not species) characters are distinct: the form of the mediodorsal process of the mantle (p. 209), the more pointed posterior end, the slightly violet tone and the looser distribution of the chromatophores; also, a more delicate tissue which is difficult to describe. But even in this and the following stages the species cannot be determined with certainty; this is only possible with half-grown specimens, except when the occurrence itself provides the answer. The typical distribution of chromatophores in the youngest stages is the same as in Loligo.

213 e. VARIATION OF THE TYPE OF ALLOTEUTHIS

In addition to "Loligo" sumatrensis Orb., 1839 (cf. Appellöf, 1885), Alloteuthis contains two Mediterranean species, A. media and A. subulata. A. media occurs only in the Mediterranean, while A. subulata is found also in the Atlantic Ocean and is abundant in the North Sea. Both species show a wide variety of forms, which explains the systematic confusion (see literature, p. 207). Each species undergoes a marked development (Figures 88, 96, 97). Further, the sexes differ markedly in size and proportions. This dimorphism, however, is very similar in both species, and only the extreme cases deviate from the vague typical character (Figures 104, 96, 97). Finally, both species are very variable; the differences between them are so indistinct that even a rich material may not permit a clear distinction. Nevertheless, comparison of the extreme cases shows clearly that there are specific differences. It was therefore necessary to determine the characters of the extreme forms which are alternative for a certain sex, or, if not for all specimens, at least for certain developmental stages.

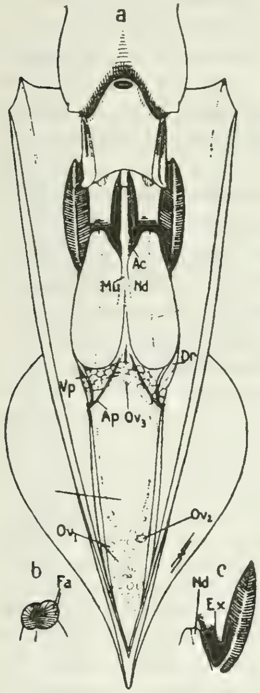

FIGURE 99. Situs of mantle cavity of a mature female Alloteuthis media, natural size. Compare with Figures 84 and 85 and note the different position and form of the nidamental (Nd) and accessory (Ac) glands. b) shows the opening of the nidamental gland; c) oblique view of gill bases, showing the opening of the oviduct (Ex). Also note the posterior pallial arteries (Ap) and veins (Vp); the oviduct (Ov_2, Ov_3) in its characteristic course; its opening into the coelom, which has just received an egg (Ov_2); the caecum, visible in the form of a large sac in the bend of the oviduct (not lettered):

Mu — musculus rectus abdominis; Dr — oviduct gland; Fa — folds of the nidamental gland.

214 It had first to be determined whether the very variable proportions of the body (Figures 97 and 108) are constant in the species, for instance, the apex of the body and the relative length of the fins. It soon became clear, however, that these characters overlap almost completely. Together with the animal shown in Figure 104a, there are specimens in which the tail is shortened to a varying degree, while all other characters are similar, to the extreme state shown in Figure 104d, which also shows a mature animal with well developed spermatophores. The shortening of the tail is accompanied by a similar shortening of the fins. These proportions alone are obviously useless for a determination of the species. The maximum and minimum values of the relative length of the fins of adults are found in the same species and sex (males of A. subulata).

However, distinction was only possible when the comparison was extended to a number of characters, mainly of the arm apparatus; immature specimens were excluded and sexes and material from different localities were treated separately. The differential characters are summarized in the table given below. I came to the conclusion that my material consisted of two distinctly different groups which deserve species rank if the extreme variations are considered (Figures 96, 97, 104). It became clear that the range of variation of most characters was overlapping although departing from different norms, and that each group consisted of a number of different varieties which I could not clearly define. That these groups are species was confirmed by the fact that one of the forms from Naples closely resembles the Atlantic form, while the other is restricted to the Mediterranean, at least it has not yet been found elsewhere; further, intermediate forms are rare, while the characteristic forms are common. Among hundreds of specimens I found only a few doubtful forms which may be hybrids. This is perhaps a case in which a natural separation of the two species begins (cf. p. 12).

In each sex and species, there are slenderer and stouter specimens, animals with a shorter or longer posterior end, with larger or smaller suckers and tentacle clubs, shorter or longer fins (see figures). In both species, however, the males are more slender and delicate. The males have a smaller posterior body with similar proportions of the head,* larger arm suckers, smaller, more delicate tentacles and a longer tail. Except for the tail, the males are generally smaller than the females (see the following table).

215

DISTINCTIVE CHARACTERS

Alloteuthis media	Alloteuthis subulata
Mantle with different chromatophores, larger chromatophores forming distinct spots between the small ones (formol preservation)	Mantle with chromatophores of equal size and almost uniform distribution at the same preservation (very relative)
Tentacles long, in fresh specimens reaching 1–2 lengths of the club beyond posterior end, when folded back	Tentacles short and delicate, not reaching the posterior end when folded back
Club large, with large suckers; width of largest suckers 7–11 times contained in width of head. Suckers of arms also markedly larger than in A. subulata.	Club small; width of largest suckers 12–16 times contained in width of head. Suckers of arms also much smaller than in A. media.
Tip of tail not longer than 6 mm in mature males and females, usually only 2–4 mm long, more pointed than in A. subulata.	Tip of tail to 2 cm in females, to 6 cm in males, at least 6 mm in mature short-tailed specimens, in which the fins are also strikingly short (Figure 104d).
Median row of hectocotylus with 10–12, usually 11, normal suckers, followed by coarse "papillae."	Median row of hectocotylus (in Mediterranean specimens) usually with 15 (13–16) normal suckers followed by fine papillae. Northern form: median row with only 9–10 normal suckers in larger specimens.

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* Even the most carefully preserved specimens do not retain the exact proportions of the living animal. In alcohol-preserved specimens, contraction of the tail makes it always more slender and pointed than in living specimens (cf. Figures 96 and 97). This should be remembered during examination of preserved material.

f. ALLOTEUTHIS MEDIA (L., 1758) Naef, 1921

DIAGNOSIS

Tip of tail at most 6 mm long. Tentacles long, strong, when folded back, reaching by several lengths of the club beyond mantle. Clubs with large suckers contained 7–11 times in width of head.

LITERATURE

Rondelet, 1554, p. 508 Loligo parva = Linné, 1767; Sepia media. Linné refers to Rondelet, whose name is therefore valid. The illustration by Rondelet reproduced here is not perfect, but it shows a distinctive character, the long tentacles with their large clubs. This is not the case in A. subulata, the tentacles of which are strikingly slender, especially in the Mediterranean form. An exaggerated drawing would stress this character instead of showing the opposite. Rondelet obviously described the Mediterranean species, like the following authors:

216 1784 Schneider Teuthis.
1789 Bruguière Sepia media L.
1816 Cuvier petit Calmar.
1817 Leach Loligo parva Rond.
1826 D'Orbigny L. subulata Lam.
1831 Delle Chiaje L. subulata Lam.
1839 Férussac and D'Orbigny L. parva Rond.
1837 Vérany L. marmorae Vér.
1840 Vérany L. marmorae Vér. (Fig. 17).
1849 Gray Teuthis parva Rond. pars.
1851 Vérany L. marmorae (Plate 37, Figs. b and f.).
1855 D'Orbigny L. parva Rond. pars.
1856 Steenstrup L. marmorae Vér.
1869 Jeffreys L. media L. pars.
1869 Targioni-Tozzetti L. marmorae.
1879 Tryon L. media L. pars.
1886 Hoyle L. media L. pars.
1889 Posselt L. media L. pars.
1890 Norman L. marmorae Vér.
1890 Carus L. marmorae Vér.
1896 Jatta L. marmorae Vér.
1893 Joubin L. media L. pars.
1907 Massy L. marmorae Vér. pars.
1908 Pfeffer L. marmorae Vér.
1912 Naef Teuthis media L.
1916 Naef Acroteuthis media (L.) Berry.
1920 Wülker (Red Sea, p. 56) Loligo (Alloteuthis Naef) media L.
1921 Naef (p. 537) Alloteuthis media (L.).
1921 Grimpe (North Sea, p. 299) (?) Acrololigo media (L.).

This species is quite common in the Bay of Naples. It is found on the fish market together with young Loligo vulgaris, sometimes with small L. forbesi or the following species. Fishermen call it "Calamariello co'o culo appuntuto."

Figures 96 and 97 show the form of the mantle in live specimens. Young stages have a cylindrical mantle ending posteriorly in a short point. This

217 becomes increasingly spindle-shaped in older specimens, although in fresh specimens it is not as pointed and slender as in Figure 102b. (This is caused by the strong contraction of the mantle during the preservation, as shown in Figure 97.) At any rate, the posterior end of the body is clearly defined from the rest of the mantle also in live specimens since the fins surround the end usually by narrow ridges and not as broad surfaces (Figure 101). Even if the fins are slightly widened (Figure 97b), they form a distinct point on the other part of the fins. This point is generally slenderer and longer in the male. The tip of the tail with the adjacent ridges is at most 6 mm, usually less than 4 mm long in males. The slenderest apex is shown in Figure 102b.

(216)

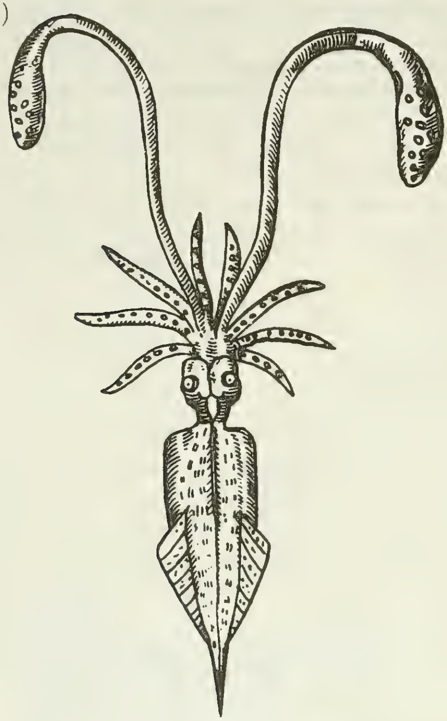

FIGURE 100. Original figure of Rondelet. (Rondelet: De Piscibus, Liber XVII, p. 508, "Loligo parva"). Although certainly not classical, the habitus of the genus is clearly recognizable. The tip of the tail may be exaggerated since the characterization is based on it. It is evident from the large clubs that this is not A. subulata. Compare Figure 103 (A. subulata).

218 The fins are rounded- heart-shaped, like those of A. subulata. Their length at the base is almost exactly half the dorsal length of the mantle, slightly longer in long-tailed specimens, slightly less in short-tailed specimens (as in subalata). At any rate, the minimal length is distinctly greater than that of short-tailed specimens of A. subulata, the maximum length is much less than that of A. subulata (Figures 102 and 104). On the whole, this species is more homogeneous than A. subulata.

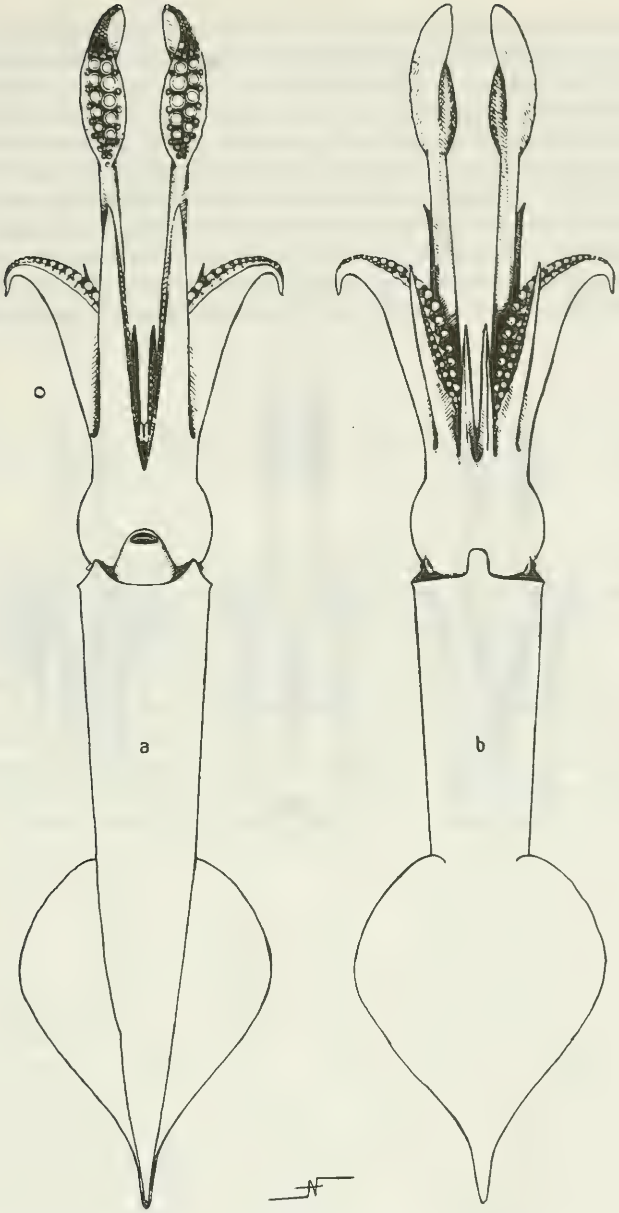

FIGURE 101. Large female Alloteuthis media, natural size, drawn from a well-preserved specimen. The figure shows the general proportions, the detailed structure of the clubs, arms, protective margins, suckers and neck fold.

The most distinct characters are found in the arm apparatus. The suckers are distinctly larger than in A. subulata, on the arms as well as on the tentacles (see figures). On the hectocotylus the heteromorphous

apical suckers are larger, coarser and fewer in number, while the median row in the proximal part has only 10–12 (usually 11) suckers. The structure of the tentacles gives the most important characters for the distinction of the two species in specimens from Naples. The tentacles of A. media are very large, with very large clubs. However, no exact measurements are given since all measurements of the soft parts are
219 inconstant. With doubtful specimens I use the following method: in typical specimens of this species the end of the club projects at least by 1–2 lengths beyond the posterior end of the mantle when folded back. This is about the maximal length of a tentacle (p. 119). It is obviously futile to use the exact length of the tentacles in preserved specimens as a character.

(218)

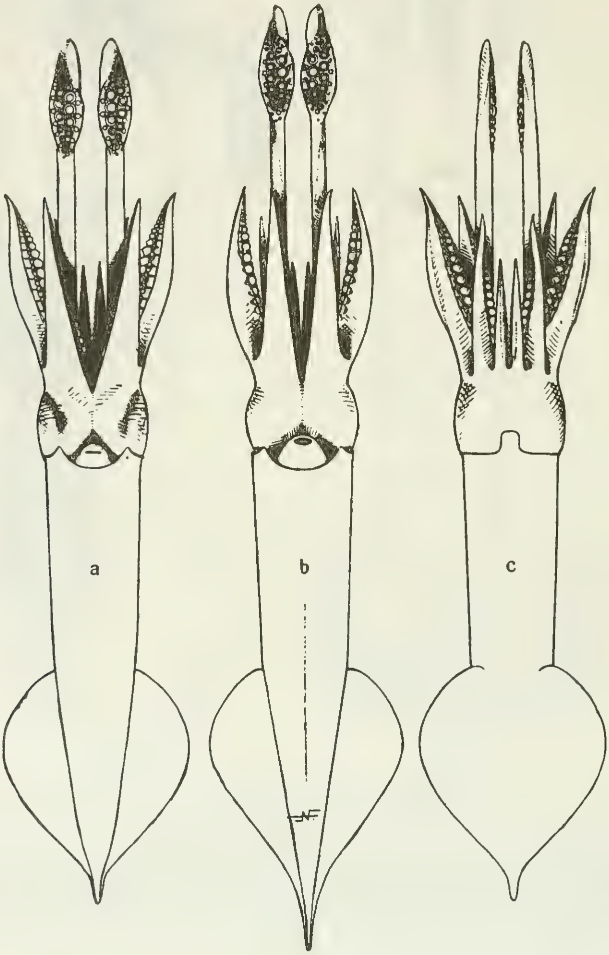

FIGURE 102. Mature male of Alloteuthis media. Figure b shows a particularly long-tailed specimen (extreme condition) in ventral view. Drawings a and c show a compact specimen from the dorsal and ventral side. After preserved specimens; natural size.

The width of the large suckers is contained 7—11 times in the width of the head, their variation is caused mainly by true variation or by variation of the suckers.

All these measurements apply to nearly or completely mature specimens, and to the most advanced young stages. A specimen like that in Figure 68 cannot be determined exactly except by intuitive distinction of vague nuances of habitus, coloration, and distribution of chromatophores. The latter is much more constant than may be assumed from the variable appearance caused by contraction of the chromatophores. Well preserved specimens of A. media show almost always a few large extended chromatophores, distributed almost uniformly between the smaller ones on mantle and fins (cf. Jatta, 1896, Plate 2, Figure 2).

g. ALLOTEUTHIS SUBULATA (L., 1798) Naef, 1921

DIAGNOSIS

Posterior point of body 2 cm long in the female and 6 cm in the male. Tentacle short, delicate, less than dorsal length of mantle also in fresh specimens. Clubs with small suckers; width of largest suckers 12—16 times contained in width of head.

This species is not as rare in the Bay of Naples as was formerly assumed, when only the large, long-tailed males were determined as "Loligo media," as Jatta did. However, it is not common and has never been caught in large numbers. I obtained many specimens, most of them in bad condition ("paranze"* material), including mature males in all the transitions shown in Figures 103 and 104, and also some mature females and numerous juveniles.

LITERATURE

The following records probably refer to Alloteuthis subulata:

1798 Lamarck Loligo subulata.
1823 Férussac L. spiralis Fér.
1823/26 Blainville L. subulata Lam. pars.
1826 D'Orbigny L. subulata Lam. pars.
1839 D'Orbigny L. parva Rond. pars.
220 1837 Vérany L. subulata Lam.
1840 Vérany L. subulata Lam. (Fig. 14).
1849 Gray Teuthis parva Rond. pars.
1851 Vérany L. marmorae pars (Plate 37, Fig. a, e).
1853 Forbes and Stanley L. media L. pars.
1855 D'Orbigny L. parva Rond. pars.
1856 Steenstrup L. subulata Lam.
1869 Jeffreys L. media L. pars.
1879 Tryon L. media pars.
1880 Tiberi L. subulata Lam. pars.
1885 Hoyle L. media L. pars.

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* Pairs of sailing fishing boats which operate with large dragnets on muddy-sandy ground.

1889 Posselt L. media L. pars.
1890 Norman L. media L.
1890 Girard Teuthis media.
1890 Carus L. media L.
1893 Joubin L. media pars.
1896 Jatta L. media L.
1907 Massy L. media L.
1908 Pfeffer L. media L.
1912 Naef Teuthis subulata.
1916 Naef Acroteuthis subulata (Lam.).
1921 Naef Alloteuthis subulata (Lam.). (System p. 537).
1921 Grimpe Acrololigo subulata (Lam.). (North Sea p. 299).

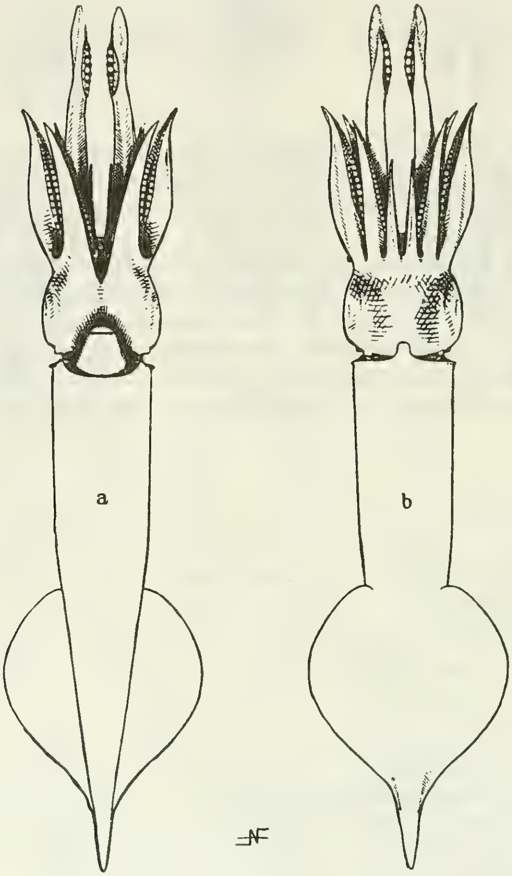

FIGURE 103. Alloteuthis subulata Lam. Mature female, natural size. Note the general proportions of the body, fins, and arms, particularly of the tentacles. Compare with Figure 101. This is the largest specimen from Naples, but even larger specimens with longer tails probably occur there as in the North Atlantic. (The protective margin of the 3rd arms and clubs is folded over.) Preserved specimen.

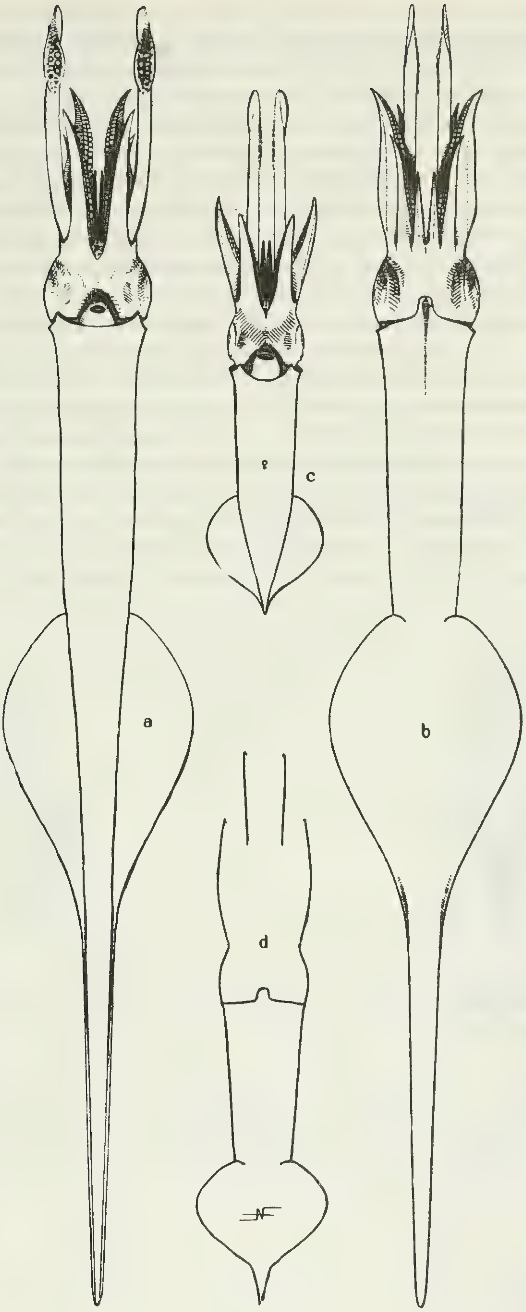

FIGURE 104. Alloteuthis subulata, natural size:

a, b – a very long-tailed, mature male from Naples; a – ventral; b – dorsal. Proportions of the head part as in the preceding figures. Note the form and proportions of the extremely long posterior part of the body; c – young female, hardly distinguishable from A. media except by the club (large suckers $^1/_{15}$ of width of head); d – mature but probably not fully grown, extremely short-tailed specimen (outline).

To understand the distinctive characters of this species it has to be remembered that they develop from juvenile conditions closely resembling those of A. media (Figure 68). Also the characteristic tail appendage does not develop at an earlier stage than in A. media. The tail of the female is never large, even if the largest of my specimens from Naples (Figure 103) is not an extreme. The true caudal appendage, i. e. the part of the posterior body where the fins form only narrow seams or ridges, is about 9 mm long. (It is sometimes 2 cm long in northern specimens.) In mature males (with full
221 spermatophore pocket) it is at least 5–6 mm long, and there are all transitions to a length of 6 cm. The appendage undoubtedly grows further in the mature animal, but perhaps only a little. It could not be determined to what extent these differences between mature specimens are due to variation or age. At any rate, the shortest-tailed animals stand at the beginning, the longest-tailed at the end of the individual and specific metamorphosis. It is necessary to bear in mind that there is no terminal growth. The appendage is only the posterior part of the body, supported by the flag of the gladius which grows at the anterior margin, while its posterior end is being gradually pushed posteriorly. Only the extreme apex contains the cone with the rudimentary rostrum (p. 171), which is not very large. The appendage contains further the pointed, conical flag of the gladius, which is narrow at this point (cf. Vérany, 1851, Plate 37, Figure e; Jatta, 1896, Plate 18, Figure 8).

(223)

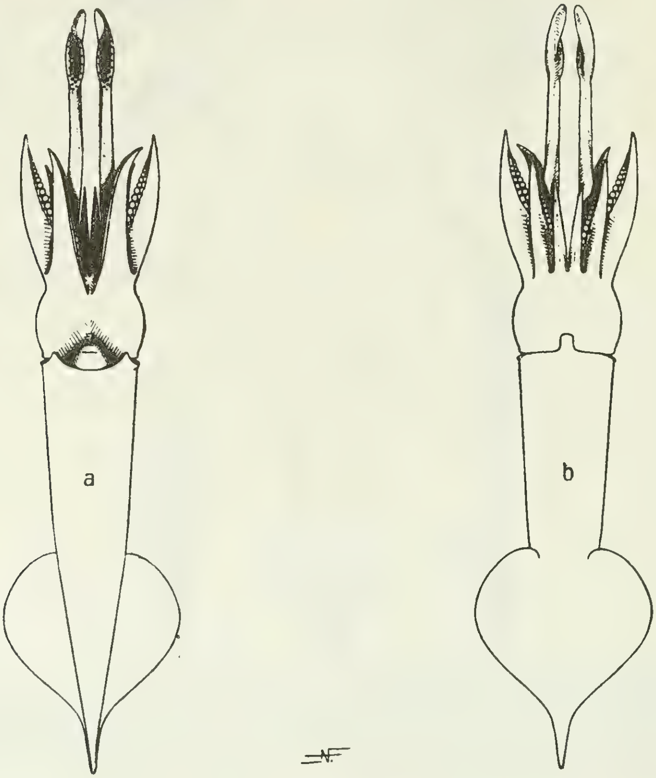

FIGURE 105. Alloteuthis subulata Lam. Mature, short-tailed male, natural size, resembling that shown in Figure 104d. Note particularly the very delicate clubs and compare with Figure 102.

The narrower the flag (relatively), the greater the possible length of the appendage. As the appendage grows longer, it becomes also wider since its anterior end contains an increasingly wider part of the flag. In short-tailed specimens, it is more pointed, thin and sharply set off from the rest of the mantle sac, or vice versa. However, an animal like that shown in Figure 105 never attains the extreme condition shown in Figure 104a and b.

The growth in length of the posterior body in maturing specimens changes the form of the fins as well. Short-tailed specimens have very short fins, also in comparison with the female and A. media of the same size. In the others the fins grow longer as far as the development of the appendage permits and may cover more than half of the dorsal length of the mantle. The proportions of the head, however, are about the same in the short-tailed as in the long-tailed specimens so that the short-tailed specimens show a peculiar habitus (Figure 104d) which differs not less from A. media (Figure 102) than the extremely long-tailed type. The mature males of the two species can thus be determined without difficulty but not the short-tailed females, the identification of which requires a number of characters of other parts (p. 215). For an understanding of the elongation of the trunk it may be added that the tail appendage contains only the posterior part of the gonads, so that their development does not disturb other anatomical relationships. The gonads may become very large as shown in Figure 105.

The suckers are generally smaller than in A. media of similar size. This is due to ecological factors; the two species probably differ in nutrition and mode of life. Comparison of the clubs shows that the largest suckers are relatively much smaller than those of A. media (Figures 101 and 103); their width is contained 12–16 times in the width of the head. The tentacles and especially the clubs are shorter and more delicate than in A. media.
222 In fresh specimens the apex of the club does not reach the posterior end of the body, not even in the short-tailed specimens. The whole arm apparatus of this species is weaker than in A. media (compare Figures 101 and 102
223 with Figures 103 and 104).

In the males from Naples the median row of the hectocotylus bears 13–16 (usually 15) normal suckers; the smaller size of the suckers is compensated by their larger number. On the other hand, northern specimens (from Plymouth, Liverpool, Bergen, Holland) have only 9 or 10 normal suckers at this place, and the abnormal "papillae" which follow are coarser, as in A. media from Naples. In A. subulata from Naples the papillae are very delicate and more densely arranged. A. subulata thus occurs in at least 2 varieties, one Mediterranean, the other Atlantic.*

The chromatophores of preserved specimens are usually densely and uniformly distributed.** I could not obtain well-preserved, fresh specimens for a comparison of their natural coloration with that of A. media.

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* The arms and tentacles of the Atlantic form are also stronger. Both Mediterranean species probably developed from the Atlantic form, which should in this case be considered as a species.

** I selected many specimens of Alloteuthis with this character from the material preserved during my absence. All of them were A. subulata.

224 *Chapter 9*

METATEUTHOIDEA OEGOPSIDA
(d'Orb., 1845) Naef, 1921

Contents: a. Diagnosis. – b. Typical structure of the adult animal. – c. Typical postembryonic development (p. 233). – d. Variation of the type of Oegopsida (P. 236).

a. DIAGNOSIS

Primary eyelid wide open or contracted only temporarily into a narrow opening at the point of the "sinus." Postembryonic forms at first with only 6 well developed arms, some of them with only one sucker; LV and V arms inhibited, developing later, often maximal. Some suckers modified into hooks during postembryonic development. Embryos without distinct yolk sac.*

This group contains the types classified by Chun (1911) and Pfeffer (1912) as Oegopsida, except Lepidoteuthis Joubin, a form of uncertain position since only fragments are known (cf. pp. 149 and 166). As the diagnosis shows, they form an ontogenetically well defined type of Decapoda, in contrast to the M. myopsida (p. 165) (see also pp. 151 and 154).

b. TYPICAL STRUCTURE OF THE ADULT ANIMAL

The general habitus of the Oegopsida varies markedly, often to a fantastic extent, both in the adults and in the juvenile forms. Only the freshly hatched
225 larvae show a more or less uniform character. But some forms in the older stages of different genera are so similar that it is not difficult to establish the typical. This is evident from a comparison of Figures 53 and 65, and does not markedly differ from that of all Metateuthoidea. This form is found in young Gonatidae, Enoploteuthidae, Onychoteuthidae and Ommatostrephidae. Also the habitus of adult animals of these families still closely resembles the general type, but the arms have to be assumed to be much longer than in Figure 53. The ancestral form of the Oegopsida was

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* To these general characteristics are added in most forms the following characters, which also apply to the diagnosis of the family although they are not mentioned: 1. The rhomboidal- heart-shaped fins (p. 163, Figure 65), with slight variations; 2. The narrowly triangular form of the funnel supports (p. 308, Plate IV, Figures 1–2) which varies only slightly; 3. The buccal funnel, which consists of 7 parts and (except Ctenopteryx – q.v.) lacks suckers; 4. The absence of accessory nidamental glands (except in the rare genus Ctenopteryx); 5. The biserial arrangement of suckers or hooks on the arms (except: Joubiniteuthidae, Benthoteuthidae and Gonatidae). These almost general characters have been omitted from the diagnosis of the families to avoid repetition and stress the distinctive characters.

thus slender, with large, terminal, transverse-rhomboidal to heart-shaped fins, pointed posterior end, rounded, dorsoventrally flattened head, slender arms and strong tentacles. Like all Metateuthoidea, this "Protoegops" was probably a permanent swimmer with a social mode of life. In contrast to the Metateuthoidea myopsida (p. 150), we assume that it inhabited the open sea, far from the coast and bottom and entered deep water (luminous organs). The Oegopsida contain the best swimmers of all Cephalopoda, the species of the genus Stenoteuthis (see below), the habitus of which closely resembles the ancestral form outlined above.

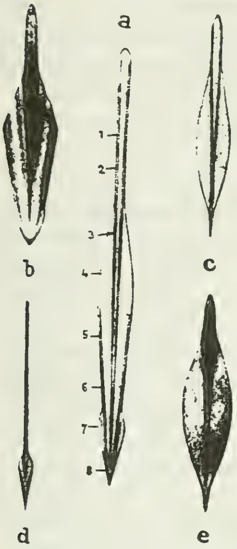

FIGURE 106. Main types of gladius in the Oegopsida.
a) Gonatus fabricii, young form, 5/4× (cf. Figure 115);
b) Abralia veranyi, natural size (after Pfeffer, 1912, Plate 16, Figure 7);
c) Teleoteuthis intermedia, 3/2× (after Pfeffer, 1912, Plate 2, Figure 6);
d) Brachioteuthis riisei, natural size (after Pfeffer, 1912, Plate 25, Figure 5);
e) Pyroteuthis magaritifera, natural size (after Pfeffer, 1912, Plate 19, Figure 21).
Note the variation of the different parts. The cone (8) varies from flat and spoonlike to conical; the rostrum (9) may be absent or strongly reduced, despite the thin sheath of the cone. The cone flag (7) may pass gradually into the flag (lateral plates (4, 6)) (c, e). The rhachis (1, 2) differs markedly in relative length and width, from sharp to blunt. The flag may be reduced (d). Compare the structure with Figure 62 on p. 146; the position in the body and the topographic relationships with those in Figure 65 on p. 153. The general structure of the gladius is typical for all Metateuthoidea. The gladius (if parts are not reduced) consists of rhachis, lateral plates, cone flag, cone, and a usually indistinct rostrum.

The relationships between mantle and shell of Protoegops are assumed to resemble those of the Loliginidae (Figure 66b on p. 157), although the postembryonic growth of the muscular mantle around the gladius does not take place at such an early stage as in the Loliginidae, but is gradual and often remains incomplete (p. 164). In Pyroteuthis (Figure 127), for example, not only the rhachis but also the flag (lanceola) is visible dorsally through the skin; the lanceola is covered only by a thin shell fold, while the muscular mantle is still attached near the lateral margins. The typical surrounding growth is not complete even in mature animal and at least the keel of the rhachis (Figure 122) is still visible through the dorsal
226 skin. Another difference between Oegopsida and Loliginidae is that the free rhachis of the Oegopsida is relatively much longer, at least in the young stages in which it occupies about the anterior half of the gladius, while the flag occupies the posterior part of the mantle sac (cf. e.g. Ctenopteryx). This proportion, however, apparently changes gradually while the fins grow anteriorly (Figure 106) and may be reminiscent of the earlier relationships shown in Figure 62. At any rate, the forms with a flag which grows far anteriorly at a later stage should not be connected with the much more ancient Mesoteuthoidea without a free rhachis (Beloteuthis).

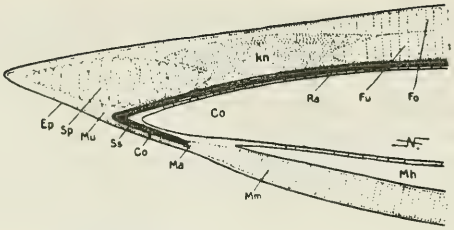

FIGURE 107. Sagittal section through the posterior part of the body of Illex coindeti. Magnified, diagrammatic. Note the rhachis (Ra) as a dark line; cone (Co); muscular mantle (Mm), attached to the free margin of the cone at Ma; the fleshy posterior point of the end (Sp) behind the cone; anteriorly, the fin cartilage (Kn) and the fins (Fl), which become later fused (secondarily) in the middle; coelom (Cö), mantle cavity (Mh); subcutaneous musculature (Mu); shell sac (Ss); epidermis (Ep); lower (Fu) and upper (Fo) muscular layers of the fin.

Above all, the gladius of Protoegops still has a well developed cone (Figure 106) on the free margin of which is the primary insertion of the muscular mantle. The early stages have a spoon-shaped conus (Figure 67 on p. 161) about as it has to be assumed for the belemnites and which does not progress much beyond this indifferent state in many Oegopsida (Figure 86 on p. 107). In other, typical Oegopsida it finally develops into a pointed hollow cone as in Prototeuthis and Metateuthis (Figure 53 on p. 136 and Figure 65 on p. 153; cf. Gonatidae, Onychoteuthidae, Pyroteuthis and Ommatostrephidae). This cone is not quite terminal but bears dorsally a fleshy apex into which projects the rudimentary rostrum inherited from Metateuthis. Such an apex is characteristic for the Oegopsida, but is also present in the Loliginidae in rudimentary form and forms in Alloteuthis the end of the tail as far as the reduced rostrum (p. 171) extends (cf. also p. 209). A fleshy apex is often present also in Oegopsida in which the rostrum has disappeared. In this case the fleshy apex is supported by a characteristic structure (Figure 107) which is situated behind the cone and mantle sac and apparently lengthens it (cf. Abraliopsis, Figure 137). The fleshy apex is a special structure, not part of the muscular mantle.

As in all Oegopsida, the fins of the young stages are separate and typically articulated with the gladius flag (Figure 157). During postembryonic
227 development (p. 161), they become contiguous and fused, at least posteriorly, into a single muscular plate the form of which is intermediate between heart-shaped and transverse-rhomboidal (Figure 65 on p. 153). The posterior end is distinctly pointed; its lateral margin forms a wide, blunt corner, the anterior margin an arc, open posteriorly and forming a conspicuous "earlobe" at its connection with the mantle on each side.

The median fusion of the fins markedly restricts the articulation with the gladius. In the Oegopsida the fin cartilages too (Figure 36 on p. 107) often become fused with each other and with the mantle (or with the posterior end of the body). This secondary condition may not have existed in Protoegops.

The mantle margin shows the three typical corners and the neck folds the pattern typical for all Teuthoidea (Figure 53 on p. 136): two transverse folds and 4 longitudinal folds between them; the third fold from above bears the olfactory papilla. The eye region does not differ from the characteristic condition of all Teuthoidea and of the Dibranchiata in general (p. 155), especially the wide-open primary lid. However, this condition is permanent in the Oegopsida, while it is only transient in other types.

The lid margin of the adult animal is no longer rounded; its thickened, immovable anterior part bears a sharp indentation ("sinus") resembling the corner of a human eye, while its posterior part is delicate, movable, and ends almost transversely in a nearly straight line. If the lid is contracted, it forms a ⊢-shaped slit, and the more or less transparent posterior margin is drawn toward the sinus and over the lens. The posterior margin then forms temporarily an incomplete "cornea" on the lens (cf. pp. 165 and 173).

The lens is very large and prominent (Plates III, IV, V, XIX) and in direct contact with the seawater in the normal position (cf. p. 175).

On the ventral and dorsal side of the head are situated the characteristic "windows" (Figures 96, 97), through which the eyeballs are visible even in preserved specimens. These windows are probably connected with the development of luminous organs on the eye bulb (cf. p. 159), but I cannot say anything definite about their typical structure. In many Oegopsida the luminous organs are situated on the ventral side of the eyeball (Figure 110), but they may extend forward and upward (cf. e. g. in Pyroteuthis), so that the existence of luminous organs also on the upper side of the bulb cannot be excluded.

The arm apparatus shows mainly the same proportions which we assumed (p. 158) for Prototeuthis and Metateuthis. The arms bear 4 rows of suckers, an arrangement which developed ontogenetically from the primarily uniserial and then biserial condition (p. 116). The tentacle clubs have 8 rows of suckers, at least in the hand part. However, the observed patterns may be better understood if it is assumed that the original form showed a certain variation between 2 and 4 (respectively 4 and 8) rows, as
228 is found in Sepia elegans (q. v.). The longitudinal rows of the arms are distinctly differentiated: the suckers of the median rows are more claw-shaped than those of the marginal rows. One group of families follows a conversion into hooks, in accordance with the considerations on pp. 127–132.

The swimming and protective margins of the adults are typical for all Metateuthoidea, but the much greater development of the protective margins on the ventral side of the second and third arms is remarkable (cf. Figure 126).

The clubs are formed according to the pattern of Metateuthis (p. 158), but they are changed considerably (Figure 108). 1. The stalk part of the club is extremely long, much longer than the stalk itself. The larger distal part of the "tentacle stalk" is taken up by a loose, zigzag row of small suckers and knobs. Between the suckers is an alternating pattern of hemispherical papillae or "adhesive knobs" situated opposite the suckers of the other tentacle (cf. pp. 119 and 158). 2. The carpal part bears similar adhesive knobs between every 2 suckers of the longitudinal rows, so that there are transverse rows of knobs between the transverse rows of suckers (cf. Figure 154). 3. Similar knobs are situated on the proximal section of the hand part, but only alternating in the intervals of the dorsal marginal row (Figures 169, 242, 250).

These adhesive knobs, together with the suckers between them, form the adhesion apparatus of the tentacle, which is a detachable connection of the two opposite tentacles. This permits steady guidance of the united tentacles during forward acceleration (p. 119), but only the Oegopsida have such a perfect arrangement in which it varies in different directions.

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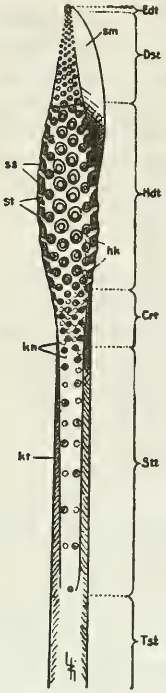

FIGURE 108. Typical structure of a tentacle of Oegopsida with a simplified quadriserial arrangement of the suckers and without modification of the main suckers into hooks. The tentacle consists of the following parts: tentacle stalk (Tst); stalk part of club (Stt); carpal part (Crt); hand part (Hdt); distal part (Dst); terminal part (Edt). The adhesion apparatus consists of knobs (dotted) on the following places: a) stalk part (kn); b) carpal part; c) hand part (hk) of club:

Kt – edgelike protective margin of stalk part; St – supports of protective margin (Ss) of hand part; Sm – swimming margin.

In the great majority of Oegopsida (as in the Metateuthoidea myopsida) the arrangement of the suckers is simpler (cf. p. 224); two rows on the arms, four on the tentacle clubs. This simpler condition, which morphologically is undoubtedly primary, cannot be considered typical because: 1) the multiserial types (Gonatus, Ctenopteryx, etc.) differ also from the others in the possession of distinctly primary characters (q. v.); 2) the multiserial types provide the best connection with the Belemnoidea, which must be considered as the common ancestral form of the Teuthoidea and Sepioidea; 3) because the latter group also has multiserial suckers (see Chapter 38). For easier orientation, however, we illustrate an otherwise typical tentacle of Oegopsida with a simplified arrangement of suckers and still without modification into hooks (Figure 108).

The buccal funnel resembles the conditions in Prototeuthis and Metateuthis. The buccal points also bear 2 rows of small suckers.

The tentacle pockets do not show the extreme development of the Loliginidae; they are shallower and leave only the base of the tentacle

229 stalks and the adjacent surfaces of the bases of the third and fourth arms free. The buccal pockets resemble those of Prototeuthis and of the Loliginidae (Figure 179) and similarly the seven buccal points with their biserial suckers (see Ctenopteryx).

A general description of the jaws and radula cannot be given here since the most different Oegopsida resemble the Loliginidae in this respect (Plate XIV), and in some cases also the Sepioidea (Figure 14 on p. 67; Plate XV). However, some details are more or less specific: 1. The lateral edge of the free biting process of the upper jaw continues on the outer plate of the proximal part as a strengthening line (Plate XVII, Figure 6). 2. In addition to a medioventral strengthening edge, the inner plate of the lower jaw bears on each side a similar edge which is situated higher and forms an acute angle with the medioventral edge near the apex of the biting process (Plate XVII, Figures 5–7). This is present in the Gonatidae, Enoploteuthidae, Onychoteuthidae, Histioteuthidae and Chiroteuthidae, but not in the Ommatostrephidae (Plate XVII, Figures 8–11).

The radula does not differ from the general type of the Decapoda [p. 122).

The funnel apparatus also shows the general character of Decapoda, but the funnel supports have a characteristic form. They are usually more or less narrowly triangular (Plate III, Figure 4; Plate IV, Figures 1–2), narrower and raised anteriorly, flat, widened, transversely truncate and cartilaginous posteriorly. They also usually show a shallow longitudinal groove. The mantle bonds are much longer and form a simple longitudinal ridge (p. 123) on which extensive gliding forward and backward is possible;
230 this is most evident in the youngest stages of many (or all?) Oegopsida, the characteristic reaction of which to strong stimuli is retraction of the head into the mantle sac. This is often also obtained by careless preservation, which makes examination difficult (see many figures). The funnel pit is sharply delimited, but not as deep as in the higher Oegopsida (Ommatostrephidae). The pit bears two pairs of adductors before the base of the funnel (cf. Onychoteuthidae or Histioteuthidae); the smaller inner adductors are vertical and more projecting, the larger outer muscles have a frontal and slightly deeper position. The adductors are typically displaced in many families (cf. e.g. Thysanoteuthis, Ommatostrephes).

The situs of the mantle cavity is as in Prototeuthis (p. 140), especially in younger animals in which the luminous and genital organs are still absent or not prominent. The following aspects are characteristic: 1. The posterior aorta is not divided into 3 main branches (one median pallial and 2 posterior pallial arteries), as is typical for the other Teuthoidea (Dibranchiata; Figure 47 on p. 124), but the two posterior pallial arteries remain united for some distance after the separation of the median pallial artery (Plate IV, Figure 1; on the characteristic origin of the genital vein in the Oegopsida see p. 155, also Naef, 1910, p. 326, Figure 4). 2. The vena cava is displaced early to the right of the middle, so that it is situated at the side of the hind intestine (Figure 109a) and is divided into venous branches, apparently not deep and dorsal to the hind intestine but superficially, ventral to it or behind the point where the hind intestine passes close to the surface. The two branching points are not homologous (see Figure 109 and compare with other superficially not recognizable characteristics, like the atypical origin of the genital artery Vol. III).

A complete characterization of the Oegopsida requires anatomical treatment. This would show how far the Oegopsida have deviated from the Teuthoidea myopsida by monotypical specialization (cf. p. 155). However, the above already proves the uniformity on the group. This general statement is also underlined by the data of the embryonic (Vol. II) and post-embryonic development (p. 233).

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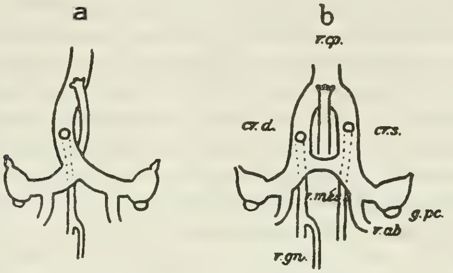

FIGURE 109. Relationship of the vena cava to the hind intestine in different Dibranchiata: b) typical condition, permanent in the Sepiolidae, otherwise found only on the embryo:

v.cp – vena cava; cv.s – left arm; cv.d – right arm, receiving the right mesenteric vein (v. ms) from the depth and joined by the genital vein (v.gn); v.ab – abdominal vein; g.pc – pericardial gland.
a) corresponding condition in the Oegopsida; c) in the Octopoda.

Of particular importance for the characterization of the group are the luminous organs, a new development which plays a major part in its ecology and classification. The typical windows on the head of the Loliginidae (p.210) and Oegopsida (p.227) suggest that their common ancestral forms (p.159) already had luminous organs on the eyeballs. However, there is no proof of the primary existence of these organs, but we have to attribute them to the Oegopsida in particular: luminous organs are typical for the group, and not only at the point mentioned but widely distributed on the body. These organs are differentiated areas of skin where luminous secretions are produced and activated by auxiliary mechanisms. They are perhaps organs for the
231 culture of luminous bacteria as Pierantoni (1918) suggested for the Sepiolidae (q. v.)*

It must be assumed, at any rate, that the ancestral form of all Oegopsida had very simple luminous organs which were distributed more widely than is observed in any recent species. It is difficult to decide whether the luminous organs developed from the accessory nidamental glands (cf. p. 126 and the Sepiolidae). The isolated occurrences within the Oegopsida can be interpreted by differentiation and specialization. Together with Pfeffer (1912, pp. X and XI) we assume the following categories of luminous organs in the Oegopsida:

1. Organs of the surface, in form of small warts scattered on mantle, head and arms, especially dense on the ventral side (e. g. Enoploteuthidae).

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* This was communicated by Prof. P. Buchner. I find it most acceptable, especially because it provides a possibility for a phylogenetic derivation. It is very likely that luminous bacteria settled "accidentally" on the skin. The differentiation of suitable skin areas agrees with the general experience on systematic phylogenetic sequences. Compare Concluding Chapter II.

2. Organs of the eyes, which may be present on the anterior, anterior-dorsal and especially the ventral side of the eyeball and visible through the windows of the wall of the eye chamber. These organs are larger than the surface organs and are often fused into a large organ on the ventral side. The primitive form of this condition may be a diffuse luminescence of the whole skin of the eyeball.

3. Organs of the mantle cavity ("ventral organs"), larger luminous tubercles situated in the mantle cavity (on the abdominal complex) and visible when the cavity is opened (Figure 128). In the living animal they emit light through the mantle. Such organs are found a) near the anus (Figure 110), typically in pairs on the right and left side (see also Onychoteuthis and Pyroteuthis); b) in the posterior part of the ink sac, more or less invaginated at the point of the accessory nidamental glands; cf. Chiroteuthis (Plate IV, Figure 3), Onychoteuthis (Plate IV, 232 Figure 1), Ctenopteryx (Plate III, Figure 4) and Octopodoteuthis (Figure 166); c) on the gill bases (Figure 110; see also Pyroteuthis, Figure 128); d) in the middle behind the renal papillae (Figure 110); e) in the middle on the posterior part of the visceral sac (Figure 128).

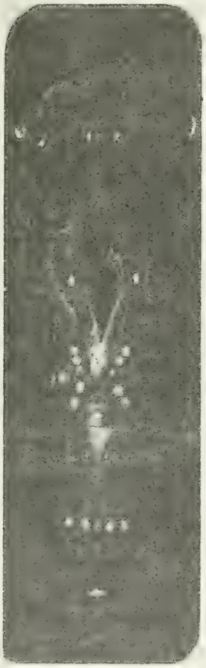

FIGURE 110. A living Lycoteuthis diadema, (Enoploteuthidae) after C. Chun (Oegopsiden, 1910, Plate 2, Figure 1) 2/3×. The luminous organs emit light of different colors: the anal organs emit red light, the middle of the 5 transverse and 5 longitudinal organs on the eye bulb blue light, the other organs white light. Note the delicate, transparent, but otherwise typical body.

The distribution of these organs in the different parts of the system is discussed by Berry (1920, pp. 149—158), who also described their function in the living animal (ibid., pp. 159 ff.). Chun (1911) deals with their detailed structure, but his views on their significance are not always correct (see the anatomical and ecological part of this work).

All these organs begin to develop in the larvae and reach their full development at a rather late stage. They are cutaneous structures, and the superficial organs are correlated with the large chromatophores. A chromatophore may cover the entire luminous organ and thus suddenly delete its effect. Such correlations may have localized the luminous organs and perfected an originally diffuse luminosity.

The sexual dimorphism of the Oegopsida shows no special characters, at least not for the group as a whole. The typical genital arm is the left V arm; its special characteristics are little known, but the modification is restricted to the apex and may be small. The different differentiations of this part of the V arm in some genera (sometimes none) suggest that they developed independently. The genital processes should be assumed to be paired in both sexes, although this is known only for the male Calliteuthis (q.v., cf. p. 154). In the male, these processes project from the
233 wide-open genital pocket (Chun, 1911, p. 35) (Figure 128), from which a caecum of the genital duct usually also protrudes.

The accessory nidamental glands are also typical, although I could find them only in Ctenopteryx (q.v.). The specific form of the nidamental glands is shown in Figure 207 (Ommatostrephes sagittatus).

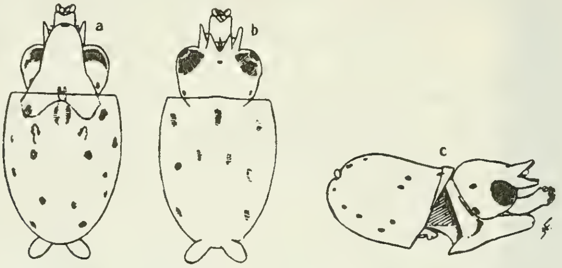

FIGURE 111. Very young stage of a species of Ommatostrephidae (q.v.) from the Naples deep-sea plankton (cf. the advanced embryos in Vol. II, Plate XI) 15×. Dorsal and ventral views, reconstructed from drawings of a living animal. The lateral aspect is based on a preserved specimen after unsuccessful cocainization. However, the fins should project further laterally (as in Figure 88). a) and b) show the typical habitus of a very young larva, except for the tentacles, which are fused in the middle (cf. Chapter 32). Note the 4 stumpy arms with a single sucker, the saclike funnel, the general form of the head, and the translucent gills, anus and ink sac. Such a larva is the ultimate, still viable simplification of young Teuthoidea (cf. Figure 88).

c. TYPICAL POSTEMBRYONIC DEVELOPMENT

An idea of the earliest postembryonic stages of Oegopsida can be obtained by comparing Figure 111, Figure 67, and the youngest "larvae" of Ctenopteryx, Pyroteuthis, and Calliteuthis (see also Vol. II, Plates VIII, XI, XII). These are very small, delicate animals (2–3 mm) with a saclike body, which is very extensible and variable in form. The posterior end of the body is still very blunt and is occupied by a scooplike cone, which is usually visible through the skin in fresh and preserved specimens (Figure 67). Also visible is the gladius, anteriorly as a narrow rhachis, posteriorly in the form of a wide, leaf-shaped flag (lanceola), which is connected directly with the cone. The anterior margin of the mantle shows hardly a trace of the 3 typical corners.

As in the youngest Loliginidae (Figure 88), the fins are rounded, mobile lobes, markedly transverse-oblong and articulated with the end of the gladius (Figure 67 shows undeveloped, embryonic conditions; cf. Figure 173 of Calliteuthis or the youngest Ommatostrephidae on Plate XI in Vol. II).

The funnel is extremely mobile and extensible in life and projects markedly from the mantle cavity. Neck and funnel bonds are indistinct at this stage, but soon become well defined. The head resembles that of the youngest Loliginidae (Figure 88, see also the youngest Onychoteuthidae). It forms a more or less thick, square plate the anterior corners of which are
234 occupied by the eyes, while the posterior corners, the "cheeks," contain the main mass of the white body. The flat, oval olfactory papillae are situated ventrally. The primary lids are wide open, with a round opening, without a sinus*; the lenses project markedly obliquely anteriorly. Particularly characteristic are the arms. At first there are only 3 pairs of very short appendages, the D, DL and T arms. The tentacles still resemble strikingly the normal arms at this stage (p. 115) and always bear a large number of "anlagen" of suckers, the largest of which are already functional, while the other arms usually have only one functional, and at most 1—3 "anlagen" of suckers. These stages are therefore "larvae," a name which is used by Chun (1911) and Pfeffer (1912) for the later stages as well. This reduced number of arms is due to an inhibition of the development of the LV and V arms, which are often present as small rudiments (Figure 67, va). They soon grow and develop suckers, but lag behind the other arms for a long time (Figures 139, 147, 173, 215, etc.).

The parts of the buccal funnel are hardly recognizable. On the other hand, the two lips surround the usually markedly projecting mouth cone (Plates III and VI show later stages).

The situs of the mantle cavity of these larvae resembles that of young embryos of Sepioidea, although the existing parts are differentiated according to their function. The gills, for example, are quite rudimentary, with 1—3 lamellae on each side (Figure 111). They remain very small and short much later; their attachment to the mantle occupies only the most basal part of the branchial axis (Vol. II, Plate XVII). Otherwise, the relationships resemble those in the Loliginidae (Figure 88, p. 188).

I will not describe the whole hypothetical series of development, but give only a description of the general phenomena which could lead to the adult ancestral form of the Oegopsida, on the basis of the existing data on the recent descendants. The posterior end of the body becomes gradually more pointed, not only relatively (because the cone grows only longitudinally, not in width) but also absolutely, because of the development of the fleshy posterior apex on the cone (p. 226) into which the growing rostrum penetrates (Figure 112). The posterior margins of the fin bases become contiguous at this point which determines the further development of the region (p. 153; Figure 65). The fins remain rounded for a long time. They become quite terminal later, but also continue to grow forward (p.161), which is made possible by the loose articulation with the gladius. The gradual entry of the 235 muscular mantle (p.163) between the two organs does not inhibit this (Figure 66 on p. 157). As in the Loliginidae, the fins continue to grow on the mantle, with which they remain articulated (Figure 120), and the "fin form" becomes typically heart-shaped – rhomboidal. The "earlobes" which are absent in the young stages, are formed at last (Plate V, Figure 3; many figures). Also, the anterior margin of the mantle and the funnel assume their typical form; the funnel bonds (Plate IV, Figure 2) and neck bonds (Figure 147) become differentiated on the funnel. The eyes, originally directed anteriorly (Figure 88), move gradually to the sides; the primary lid margin, which is at first rounded, attains its typical outline (Figures 150, 156). The rudiments of the buccal points (Plate VI, Figure 1) become more distinct; the dorsal pair of the 8 rudimentary points become fused at an early stage (as in Sepia – Vol. II, Plate VI, Figure 2; Plate XXI). But mainly the arm apparatus attains its definitive form. Both pairs of the at first rudimentary dorsal arms reach and even exceed the size of the other pairs. In the typical ("primitive") Oegopsida the arms usually show the formula 3, 4, 2, 1. At the same time, there is a progressive formation of new suckers in one row which are, however, immediately displaced to the right or left, so that many of the uniserial arrangements of "anlagen" of suckers are usually not present (as in the Sepiidae – Vol. 11, Plate XXI; see also the hectocotylus of Tremoctopus; compare, however, the development of the tentacle clubs in the Ommatostrephidae). True suckers begin to develop at first on all arms and the tentacle clubs, but the suckers which later become hooks usually do not attain their full differentiation (Plate XII). Their development is at first inhibited and they become hooklike suckers and finally true hooks without passing through the stage of clawlike suckers (but cf. Gonatus). The clubs also grow distally, so that the few pairs of first formed suckers are later situated on the proximal end of the stalk part (see figures in the Onychoteuthidae). More suckers are formed on the carpal, hand and distal parts of the club as the apical growth of the club continues (which acts as a vegetative center; see p. 107). Thus, the few suckers on the club of Octopodoteuthis (q. v.) belong not to the hand part but to the stalk part, because the hand part is completely suppressed. The function of the suckers involves a division of labor and a gradual change of functions 236 (comparable to the legs of Crustacea) which is accompanied by the modification of the suckers. The suckers of the club of the larvae (i. e. of the later stalk part) are always biserial and for a long time larger than those of the undeveloped hand part. Since the younger "larvae" of Oegopsida have no hand and distal part, there is also at first no swimming margin. The same applies to the arms of the larvae. The protective margins appear later. The supports appear first, vaguely resembling isolated cirri (p. 91, also Figure 23; cf. Abraliopsis, p. 292).

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* Because of the delicate structure of the lids, the eyes bulge slightly, causing a widening of the lid margin, which becomes contracted at the base of the eyeball during fixation so that the eye becomes more prominent and marked off by a constriction. Such deformations are frequent in badly preserved specimens, and cocainization does not always prevent them either. Such a specimen is shown on Plate IV (Figure 2) to demonstrate the topography of arms, eyes and head. Compare also Figure 141 (Abraliopsis) and similar deformations in other figures (e.g. in the Ommatostrephidae).

(235)

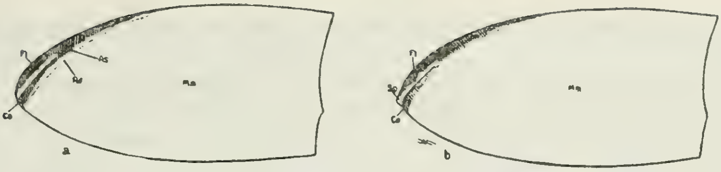

FIGURE 112. Mantle sac of two young larvae of Abraliopsis (length 4 and 4.5 mm without arms):

Mm — muscular mantle; As — attachment to gladius; Rd — margin of gladius; Co — cone; Fl — fin base; Sp — apex of body. Note particularly the spoon-shaped cone, the secondary formation of the apex of the body on the cone, and the relation between fin base and apex of body. The fins have been removed. This figure shows relationships typical for all the Metateuthoidea (p.161) and resembling the primary relationships observed in the younger stages (Figure 67 on p. 161) and in the Prototeuthoidea (p. 142).

d. VARIATION OF THE TYPE OF OEGOPSIDA

The great variety of forms of the Oegopsida makes it desirable to show their relationships in form of a genealogical tree. The numerous families established by Pfeffer (up to 1912) for their systematic order need only slight modifications to be considered as natural systematic units, but their large number suggests the establishment of higher categories.*

Material of most genera is unfortunately difficult to obtain, and the incomplete knowledge of their structure and development precludes definite conclusions on the relationship between the families. Only a few suggestions can be given here and I do not believe that the proposed groups can be systematically established.

1. There are undoubtedly closer relationships between the Ommatostrephidae and Thysanoteuthidae and this group apparently also includes the Psychroteuthidae Thiele (1921), which are less specialized (e.g. with respect to the funnel cartilage). 2. A second group contains the Gonatidae, Enoploteuthidae, Onychoteuthidae and Octopodoteuthidae, all characterized by the formation of hooks. 3. I consider the families Brachioteuthidae, Joubiniteuthidae, Chiroteuthidae and Cranchiidae to be closely related. 4. The Bathyteuthidae, Neoteuthidae, Histioteuthidae and Architeuthidae are apparently isolated families, but the Histioteuthidae appear to be related to group 2 and the Architeuthidae to group 1. At any rate, the Oegopsida known today can be classified in 15 families listed in the following natural order:

237
1. Bathyteuthidae Pfeffer, 1912
2. Neoteuthidae Naef, 1921
3. Architeuthidae Pfeffer, 1900
4. Gonatidae Hoyle, 1886
5. Enoploteuthidae Chun, 1910
6. Onychoteuthidae Gray, 1849
7. Octopodoteuthidae Berry, 1912
8. Histioteuthidae Verrill, 1881
9. Brachioteuthidae Pfeffer, 1908
10. Joubiniteuthidae Naef, 1922
11. Chiroteuthidae Gray, 1849
12. Cranchiidae Gray, 1849
13. Psychroteuthidae Thiele, 1921
14. Ommatostrephidae Gill, 1871
15. Thysanoteuthidae Keferstein, 1866

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* Berry (1920, pp. 149–153) apparently felt the same need. His systematic attempt, however, is not adequately documented and his classification differs markedly from the views presented here.

All but 4 of these families will be described in detail in the following chapters.*

For understanding the variety of forms of Oegopsida, however, the above list is less helpful than a consideration of the actual variation of the various structural elements from the typical, as we have attempted for the Metateuthoidea (p. 162). Such a study involves a comparison of entire ontogeneses, as this expresses the natural relationships better than a comparison of definite forms.** We are dealing here with a very fluid type, mainly because postembryonic development ends at an earlier or later stage although it proceeds in similar (typical) directions. Many characters are inhibitions, while others are extreme manifestations of general trends.

The growth of the muscular mantle around the shell may remain incomplete to a varying extent. Not only the keel of the rhachis but also a large part of the flag may remain free, which is typical for the young stages. Examples are the Pyroteuthinae, Histioteuthidae and all Cranchiidae (q. v.). If the chromatophores are contracted or bleached, the lanceola is visible in the preparation (dark) through the mantle, as it is only covered by the thin shell fold. As in the Loliginidae, the rhachis may be completely covered by the muscular mantle and also the keel may be indistinct (see Ommatostrephidae). The flag of the gladius often remains rudimentary
238 (Figure 106a, d), in the form of a narrow seam on the rhachis or it is quite indistinct (Onychoteuthidae, Ommatostrephidae). The cone may also disappear, since its first "anlage" is much too small and delicate to be visible on the gladius of the adult, if it does not grow further (inhibited growth). The cone may be flat, indistinctly delimited from the beginning. The rostrum is usually reduced to mere traces (only the Gonatidae and Onychoteuthidae still have a large rostrum). However, a rudimentary periostracum is formed also on the cone of other forms and may end in an easily overlooked rostrum (Ommatostrephidae, Figure 103). If the cone is flat or quite rudimentary, a fleshy apex of the body is also absent and the posterior end is blunt (Ctenopteryx, Figure 122; Bathyteuthis; Octopodoteuthis Figure 167; many Cranchiidae). The fins often lose their terminal position and their juvenile relationship at the posterior end becomes definitive, whatever their other form may be (cf. Ctenopteryx).

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* On the Neoteuthidae see p. 48, also Naef, 1921 (System, pp. 535 and 540), and especially the illustrations in Thiele (1921, Plate 54, Figures 13–14). On the Architeuthidae see Mitsukuri and Ikeda (1895, Plate 10), where a moderately well preserved specimen is correctly illustrated for the first time. The figures in Verrill are apparently drawn after the Ommatostrephidae (especially the fins). Cf. also Pfeffer, 1912. On the Joubiniteuthidae see Joubin (1916: "Chiroteuthis" Portieri). This is a very peculiar form of Oegopsida with extremely long arms with 4–6 rows of suckers (Bull. Monaco, No. 317), certainly a species of a new genus and family which is morphologically related to the Architeuthidae and Chiroteuthidae. On the Psychroteuthidae see Thiele (1921, Plate 53). The form described there has the general habitus of an Ommatostrephes (as which I identified it initially). Its gladius, however, has a typical, wide flag; the funnel bonds are simple, and the arm tips bear peculiar (luminous!) organs.

** Cf. Introduction, p. 11. As will be shown in the treatment of the Oegopsida, final conditions can only be understood on the basis of and in close connection with the preceding stages, especially because inhibition of growth is an important factor and the characters to be compared may develop prematurely in one instance and late in another. There is an ecological-morphological explanation for these inhibitions of development. The Oegopsida are Teuthoidea adapted to pelagic life. They became independent of the coast and bottom and entered the deep waters of the open sea, producing planktonic juvenile forms as an adjunct of the typical development. Slight changes are possible and often take place while the juvenile forms develop and metamorphosis is retarded.

The attachment of the fins becomes longer anteriorly to a varying extent. Except for forms with an entirely larval habitus (Bathothauma and other Cranchiidae), the fins occupy at least one third, usually about half or more of the mantle length. The fins of adult Ctenopteryx, Ancistrochirus, Cucioteuthis, Octopodoteuthis, Neoteuthis, Mastigoteuthis and Thysanoteuthis occupy the greater part of the length of the mantle (as in Sepia and Sepioteuthis). This condition is apparently the final state in the development of the fins of Decapoda. This large displacement is easily understood in view of the articulation of the fin base, regardless of whether it is based on the muscular mantle or the lanceola. A direct connection with the gladius often persists in the posterior part of the body, while the articulation pocket of the fin base is displaced farther anteriorly on the muscular mantle (Figures 137 and 185). The fins are often fused in the middle for most of their length, i. e. not only at the posterior end which is typical (Figure 167).

The neck folds may be suppressed at all stages of their development. Most constant is the 3rd longitudinal fold, which bears the olfactory papilla at the base; this fold also appears first (Figure 156). The flat-oval olfactory papilla often moves from the bottom of the fold to its crest, which increases exposure to external stimuli. The function of the fold is apparently mainly to raise the olfactory organ from the head, and all parts not related to this function become reduced, so that a "stalked olfactory tubercle" is formed (Plate IV, Figures 1 and 3) on the third longitudinal neck fold, of which only the part with the olfactory epithelium persists.

The typical differentiation of the primary lid may be suppressed (p. 235), leaving a round outline without or with an indistinct sinus in the adult. In Octopodoteuthis and in the Cranchiidae (q. v.) the prominent embryonic-larval position of the eyes persists longer than elsewhere (cf. Vol. II, Plate X, Figures 1–3; Plate IV). This condition may be even more
239 accentuated so that stalked eyes are formed (Cranchiidae). This extreme state is connected with a change of the entire supporting part of the head, without addition of new parts or disappearance of generally present parts, since the necessary conditions are already prepared in the structure of the larval head. "Windows" are only found in the larger and fleshier forms, they are not necessary in transparent, delicate species.

The great majority of genera retain the biserial arrangement of suckers on the arms, which appears in the early larvae (p. 224); the quadriserial condition is not exceeded on the clubs (exceptions: Gonatidae, Histioteuthidae, Bathyteuthidae, Joubiniteuthidae, Brachioteuthidae, Illex and Mastigoteuthis). Conversion into hooks is absent in many Oegopsida and takes place only partly in others. In Octopodoteuthis and Paragonatus, for example, it is restricted to the tentacles, in the Onychoteuthidae and Galiteuthis it is found only on the arms. The transition has to be assumed to be gradual (p. 132), i. e. the number of normal suckers formed increases, that of hooks decreases. Such a transition is clearly possible since the modification does not take place in the outer suckers of a longitudinal row (at the end and base of the arms or on the hand part of the tentacle). The number of modified or nonmodified suckers fluctuates in general in hook-bearing Oegopsida. As will be shown in the special chapters (13–15, 18, 20), there are gradations in the ratio of both types of organ not only in the families but also in the genera and species.

There are also marked differences in the development of swimming and protective margins. We assumed (p. 159) that the swimming margins of the DL arms are connected proximally with the outer edges of the arm. Such a displacement is a specialization of the most common condition (p. 118) which does not take place in many Oegopsida. There is instead a simple swimming margin restricted to the distal part of the arm (Figure 53 on p. 136) in the middle between the outer edges of the arm, if these edges are distinct (examine the figures of Pyroteuthis, Abralia, Abraliopsis and Histioteuthis).

(240)

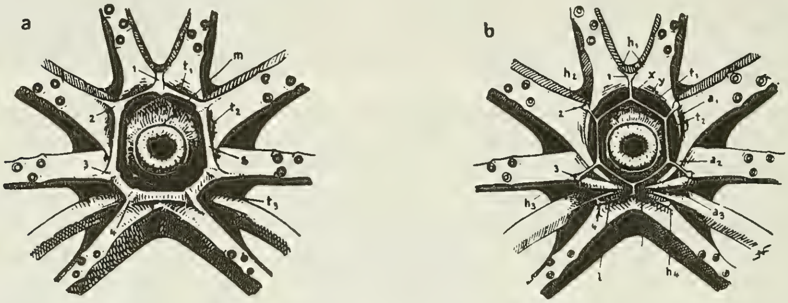

FIGURE 113. Mouth area of Illex coindeti (natural size). The figure shows the typical condition in the Ommatostrephidae. The arms are spread. The buccal pockets are exposed by removal of the buccal supports (at the base) and the connecting buccal membrane near its attachment to the mouth cone (cf. Figure 79 on p. 180). Note: the 7 supports (1–4) and bonds of the buccal funnel; the transition of the bonds into the protective margins; the connecting buccal membrane (s) around the mouth cone; the openings of the 6 buccal pockets (t_{1-3}, "water pores"); the 8 arm stumps with suckers, protective margins and supports; the connections of the protective membrane; the base of the tentacle with the vein on its inner side and the foldlike "fastening ligament" raised by it. The figure b shows the attachment of the buccal membrane on the mouth cone (y), the 6 buccal pockets (t_{1-3}), the superficial adductors (a_{1-3}) of the upper 3 arm pairs, and the base of the tentacle.

Particularly striking are the protective margins of Architeuthis and Abraliopsis (q. v.). Each sucker has still (or again) 2 supports as in Praedecapus (p. 116). Since these supports have the character of palps (p. 236), this is apparently an atavistic inhibition or a return to primitive conditions (Figure 23 on p. 91).

The general structure of the definitive club of Oegopsida and the arrangement of suckers in the quadriserial basic type are shown in Figure 108, but this type may vary in a number of ways. Except for extensive reduction (inhibition) observed in the Octopodoteuthidae (q. v.), there are often simplifications: the stalk part may be suppressed; the carpal part may be reduced to a "carpal pad" (Onychoteuthidae, Enoploteuthidae) or disappear as a special area, because its suckers remain
240 associated with the adjacent parts; the adhesion apparatus (p. 228) is then restricted to the stalk part or the dorsal row of the proximal hand part. In general, each part of the club may expand or become reduced at the expense of or in favor of the adjacent parts. The various parts of the club are formed only by differentiation of at first indifferent suckers. Some

suckers may disappear; most frequently those of the stalk part or of the outer rows of the hand part (Figure 154) disappear partly or completely. An absolute increase or decrease of the number of rudimentary suckers naturally takes place at first in the distal part, which therefore shows the greatest variation of the number of suckers. The appearance of new suckers at the apex sooner or later ceases. Conversion into hooks is always restricted to the median rows of the hand part of the club, where only a few (Gonatus) may be affected, only the ventral row (Enoploteuthidae), or both median rows (Onychoteuthidae). An atypical increase of the number of suckers takes place in the hand rows of the Histioteuthidae and Brachioteuthidae, and in the distal rows of Illex.

The buccal funnel of the Enoploteuthidae remains composed of 8 parts because the fusion of the two dorsal points does not take place (Plate III, Figure 1). In Histioteuthis, on the other hand, the ventral points become fused at an early stage, so that the buccal membrane consists of 6 parts (see also Octopodoteuthidae). As stated on p. 159, the fusion of the buccal pockets is prepared in the Metateuthoidea because the pockets are separated ventrally only by a thin septum (Figure 79 on p. 180). The buccal membrane thus invariably consists of 6 parts, even if there are 7 or 8 supports, at least at the attachment of the membrane on the mouth cone (cf. also Ommatostrephidae; Figure 113). Some types still show the primary topography between the inner edges of the V arms and the fastenings of the ventral buccal points, in which case the attachments continue into the median protective
241 margins. This is the case in the Bathyteuthidae, Gonatidae, Onychoteuthidae, and also in the Brachioteuthidae, Chiroteuthidae and Cranchiidae, which are also otherwise related to the former group. Such a condition is termed "inner attachment" (Pfeffer, 1912). Other forms developed an outer attachment which involves the lateral protective margins of the V arms (Plate III, Figures 1, 2; Plate VI, Figure 3) (Enoploteuthidae, Ommatostrephidae).

The funnel bonds are typical in the Onychoteuthidae, Enoploteuthidae, Bathyteuthidae, Octopodoteuthidae, Gonatidae, Architeuthidae, Histioteuthidae and Brachioteuthidae; the Ommatostrephidae, Thysanoteuthidae and Chiroteuthidae also belong to this category. In the Grimalditeuthidae and Cranchiidae the funnel cartilage (at least in the adults) is replaced by a fusion with the mantle. A partial fusion is observed in Symplectoteuthis together with a completely preserved bond.

The neck bond varies considerably and may be replaced by a fusion between mantle and neck (Cranchiidae).

The outer funnel adductors may be displaced laterally, especially in the Ommatostrephidae (Figure 216), less markedly in the related Thysanoteuthidae (Figure 248).

Except for the genitalia, the mantle situs shows a more or less similar topography, but the proportions may vary considerably. The genital duct is paired in the female, rarely (Pyroteuthis) present only on the left. In the male, the duct is usually present only on the left side, and only exceptionally (Calliteuthis) is it bilateral.

FAMILY GONATIDAE*
(Hoyle, 1886) Pfeffer, 1900

Contents: a. Diagnosis. – b. Literature. – c. Genus Gonatus. – d. Gonatus fabricii.

a. DIAGNOSIS

Arms with 4 rows of suckers; suckers of both median rows developing into hooks in the 3 upper pairs of arms. Tentacle clubs with at least 8 rows of suckers, some of which may be converted into hooks. Adhesive knobs alternating regularly with suckers in the proximal part of the dorsal marginal row of the hand part of the tentacle. A submarginal row of knobs also present between the marginal suckers in the stalk part of the club, on each side or only dorsally. Gladius with a long free rhachis, a small flag and a conical, slender cone with a phragmoconelike filling in its cavity (cf. p. 243).

b. LITERATURE

I am not quite certain that Gonatidae actually occur in the Mediterranean, but I use Hoyle's data to describe this very interesting group in more detail. In spite of their typical habitus (Figure 114), their special characters are mainly in the suckers, the pattern of which is representative for the Oegopsida, or even the Teuthoidea despite its isolated position. The arrangement of the adhesive organs on the club has not been adequately explained or genetically interpreted. However, it is certain that more than 8 longitudinal rows develop at an early stage on the hand part and that in this respect the Gonatidae resemble the Bathyteuthidae and other families in which the club bears more than 4 rows. The arrangement of suckers on the arms is even
243 more characteristic: already in young animals (Figure 116) all 8 arms bear 4 regular longitudinal rows, although the suckers of the ventral arms remain small for a long time, i. e. they remain in the primary condition.

According to the description of Protodecapus (p. 117), Prototeuthis (p. 136) and Metateuthis (p. 157), the quadriserial arrangement of the suckers on the arms is typical for all recent Metateuthoidea, although only isolated forms in addition to the Gonatidae show such a pattern. Our view is based on the need (p. 10) to formulate the typical relationships in the simplest manner. There are also special reasons for this.

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* I was unable to obtain Mediterranean material of this very interesting and important family (subfamily in Hoyle). The following text is therefore based on observations of North Atlantic, too small or badly preserved specimens. Compare Verrill (1881), Hoyle (1889), Pfeffer (1900, 1908, 1912), Berry (1912, 1913), and particularly Steenstrup (1881, Prof. A.E. Verrill . . .).

Proof that the Gonatidae are very ancient Oegopsida is evident not only in their habitus but also in the presence of a phragmoconelike filling (cf. Steenstrup, 1881; Hoyle, 1889; Pfeffer, 1912; Naef, 1922, Fossile Tintenfische, Figures 39 and 59). Steenstrup found in the cavity of the cone "loose chitinous layers like a stack of watch glasses" (Pfeffer, p. 230). According to Hoyle, the first-formed parts of this filling do not consist of shell substance but are cartilaginous, i. e. they contain embedded cellular elements. This does not speak against a homology with a true phragmocone, as might be assumed. Shells of Dibranchiata are often in direct contact with cartilaginous structures which probably entered the interior of the shell sac (cf., for example, the description of Appellöf of the rudiments of the shell of Octopoda, 1899). At any rate, the homology between these structures and the phragmocone can only be general.

Another indication of the ancient character of the family is the further development and modification of the armature of the arms, at least of its arrangement. We already rejected the view (p. 158) that the postembryonic conversion of suckers into hooks is a natural condition in the Teuthoidea and that there is a typical resemblance to the Belemnoidea in this respect. This conversion occurs also in certain Oegopsida which are closely related in other respects as well (p. 236), and quite independently of the Belemnoidea (pp. 127–132), under different morphological preconditions and in a distinctly different form. However, the manner in which the conversion takes place in the Gonatidae reflects a stabilized arrangement of the adhesion organs in general.

The so far normal suckers (stage in Figure 116) of the median rows of the upper 3 arm pairs become hooklike suckers and true hooks (Plate XII, Figure 9) comparatively late, and transitions are present in all stages. (Because of the scarcity of material, I cannot give a complete description.) Such a modification does not take place on the ventral arms, on which the primary form of suckers persists.

The tentacle club has a small number of hooks in a single longitudinal row restricted to the hand part, but this is not general. Berry (1912a, p. 310, Plate 52, Figures 1–2, Plate 53, Figures 1–2, Plate 54, Figures 1–4, Plate 55, Figures 1, 3–7) described a very interesting form at first as a
244 young stage of Gonatus fabricii, later as Gonatus magister (1913, Proc. Ac. N. Sc. Philadelphia, p. 75). However, the clubs of this form differ so sharply from Gonatus that I (1921, System p. 535) made it the type of the new genus Berryteuthis. This seems justified, especially because the specimens known as Gonatus fabricii probably do not belong to a single species. Berryteuthis has fins of the type of the Enoploteuthidae which occupy more than half of the mantle length. It has no hooks on the clubs, and the suckers of the club show a different, more normal arrangement; there are more than 8 longitudinal rows which do not diverge to form a bare median area on the hand part and reach proximally to the distal third of the stalk, also without leaving a bare stripe between them. The buccal funnel is stated to consist of 8 parts, as in the Enoploteuthidae (see below).

c. GENUS GONATUS Gray, 1849

DIAGNOSIS

Suckers of a median longitudinal row of the hand part of the club are transformed into hooks, including one especially large, subdistal hook. One species (but see p. 245).

d. GONATUS FABRICII Lichtenstein, 1818

DIAGNOSIS

Buccal funnel normally consisting of 7 parts. Fins reaching to about half of the mantle length only in large specimens (over 20 cm mantle length). Club with one rather large distal hook and a very large subdistal hook; other hooks small.

LITERATURE

1780 Fabricius, Sepia loligo (p. 358).
1818 Lichtenstein, Onychoteuthis fabricii (p. 13).
1843 Möller, Onychoteuthis fabricii (p. 3).
1849 Möller, Onychoteuthis amoena (p. 3).
1849 Prosch, Owenia megalops pars (Plate I, Fig. 7).
1849 Middendorf, Onychoteuthis kamtschatica (Part II, p. 186, Plate 12).
1849 Gray, Gonatus amoena (p. 68).
1858 Adams, Gonatus amoena (p. 36, Plate 4, Fig. 2).
1878 Sars, Gonatus amoenus (p. 336, Plates 17, 31).
1881 Steenstrup (!), Gonatus fabricii (p. 9, Plate I).
1881 Verrill (Bull.), Cheloteuthis rapax (p. 110, Plate 2, Figs. 1–1f).
1881 Verrill (Trans.), Gonatus fabricii (p. 291, Plate 45, Figs. 1–16, 2–2d).
1881 Verrill (Trans.), Lestoteuthis kamtschatica (p. 251).
1881 Verrill (Trans.), Cheloteuthis rapaz (p. 293, Plate 49, Fig. 1).
1881 Verrill (Trans.), Gonatus amoenus (pp. 291, 388, 300, 428).
1881 Verrill (Trans.), Lestoteuthis fabricii (pp. 291, 293, 387, 428).
1881 Verrill (U. S. Fish.), Cheloteuthis rapax (p. 286, Plate 15, Fig. 3–3f, 4).
1881 Verrill (U. S. Fish.), Gonatus fabricii (Plate 15, Fig. 1–1c, 2–2d).
1882 Steenstrup, Gonatus fabricii (p. 143).
1886 Hoyle, Gonatus fabricii (pp. 41.174).
1886 Dall, Lestoteuthis fabricii (p. 209).
1889 Hoyle, Gonatus fabricii (p. 117, Plates 13, 14).
1889 Jatta, Gonatus fabricii (p. 66).
1889 Carus, Gonatus fabricii (p. 450).
245 1891 Lönnberg, Gonatus fabricii (p. 38).
1892 Appellöf, Gonatus fabricii (p. 9).
1897 Vanhoeffen, Gonatus fabricii (p. 193).
1898 Posselt, Gonatus fabricii (p. 279).
1898 Lönnberg, Gonatus fabricii (p. 792).
1899 Lönnberg, Gonatus antarcticus (?).
1900 Pfeffer, Gonatus fabricii (p. 163).

1901 Friele and Grieg, Gonatus fabricii
1908 Pfeffer, Gonatus fabricii (p. 71).
1909 Massy, Gonatus fabricii (p. 381).
1909 Massy, Gonatus fabricii (p. 27).
1909 Hoyle, Gonatus fabricii (p. 267).
1909 Hoyle, Gonatus antarcticus (p. 267 [?]).
1912 Pfeffer, Gonatus fabricii (pp.230–42, Plate 15, Fig. 17–22).
1916 Naef, Gonatus fabricii (pp.15, 18).
1921 Naef, Gonatus fabricii (p. 537).

G. antarcticus Lönnberg is perhaps a valid species. This is certainly the case in another form described by Berry:* the description and drawing of a "G. fabricii" (which includes the form of 1912 and also "Gonatus" magister 1913, i.e. Berryteuthis – see p. 244) show that there are 8 buccal points** and that the base of the fin covers half of the mantle length already in very young specimens with a mantle length of only 24 mm. In the northern Gonatus fabricii this does not develop before the animal reaches a size about 10 times as large; in specimens of the same length, the fins would cover less than a third of the mantle length and they also differ in form (Figure 116). I therefore propose for Berry's specimens of Gonatus fabricii (excluding B. magister) the new name G. berryi.

Except for the above characters, the following description gives the typical conditions of the whole family in nearly all points.

α. OLDER SPECIMENS

The general form of the body (Figure 114) is typical for the Metateuthoidea in general and for the Oegopsida in particular. It resembles the form of the Onychoteuthidae and Ommatostrephidae so closely that Gonatus could easily be confused at first glance with Onychoteuthis or Illex (cf. figures). The consistency of the tissue is about as in Illex. Gonatus should therefore be considered as a strong swimmer and predator. The specific armature of the arms and clubs of this genus suggests a special type of prey. The skin is soft and smooth. To judge from preserved specimens, the coloration and distribution of the chromatophores are intermediate between Ommatostrephes and Illex. Violet-brown tones (on the dorsal side) may be very slight; the color of the live animal probably varies from yellowish brown to reddish brown. The chromatophores of my specimen are muddy reddish brown,

The mantle sac is slender and pointed posteriorly. The conical cone has a typical apex which reaches beyond it. Younger specimens have a translucent cone, especially when the chromatophores have disappeared (Figure 116), not only in the ventral midline but also laterally. The posterior part of the gladius is covered dorsally by the fins as far as these
246 are fused in the middle; it is visible through the skin as a narrow, dark median stripe where the fins diverge. The stripe is widest before the

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* Berry, S.S. 1912, pp. 308–312; Plate 52, Figures 3, 4; Plate 55, Figure 2.

** This character perhaps applies only to the specimens of "G. magister" which were at first not distinguished by Berry in 1912. At any rate, the characters are strongly reminiscent of the Enoploteuthidae (q.v.).

anterior margin of the fins and disappears in the anterior third of the mantle. The gladius is completely surrounded by the muscular mantle in this area (p. 164), but it is visible as a dark longitudinal stripe toward the anterior margin of the mantle.

(247)

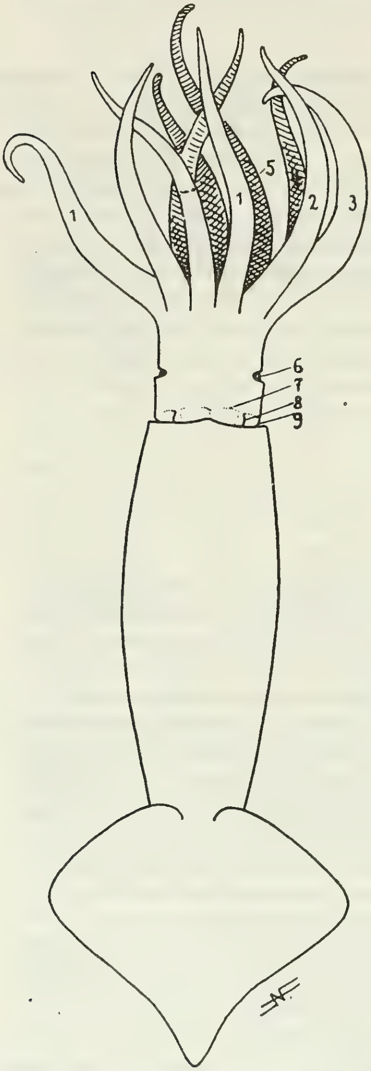

FIGURE 114. Gonatus fabricii. Outline of a larger specimen (half natural size). After Murray and Hjort (The Depth of the Ocean, 1912, Figure 98, p. 113).

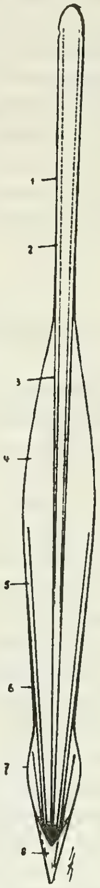

FIGURE 115. Gladius of a young Gonatus fabricii from Bergen, 2.5×. The position in the animal can be determined by comparison with Figure 116. Note the cone (8), the cone flag (7) and the large, free rhachis (1).

2 – strengthened margin of the rhachis; 3 – median asymptote; 4 – lateral plate; 5 – deposition on lateral plate; 6 – transition to the cone flag.

The gladius shows a groovelike rhachis the free anterior part of which occupies about one third of the whole rhachis. The rhachis continues posteriorly in a narrow flag (lateral plate) which is widest behind the middle of the total length and tapers gradually toward the apex without disappearing. Slightly less than two fifths of its length is still situated behind the narrowest place. The flag widens again posteriorly at the junction with the cone flag
247 and finally curves laterally and ventrally to form the cone, the ventral margin of which forms a median angular recession at the point of contact. The posterior end is pointed, without a distinct rostrum. The anterior end has the form of a slightly blunt Gothic arch. The posteriorly converging margins of the flag are accompanied by submarginal lines of deposition. The lateral margins of the rhachis are also slightly strengthened by ridges which project inward, at least anteriorly and in the middle. A median ridge is hardly indicated. The gladius is thus not completely surrounded by the muscular mantle. The rhachis is situated under the skin almost its whole length, like the cone. However, the muscular mantle covers the narrow flag completely, so that the gladius is situated in its greater part inside the mantle sac. The anterior margin of the mantle sac has the typical form but its dorsal corner is often indistinct because of contraction.

The fins are typically rhomboidal-heart-shaped and fused in their greater part in the midline (Figure 116), and then diverge suddenly. A dark median dorsal line indicates the fused fin cartilage, if the skin is worn off.

The form of the head is intermediate between the Onychoteuthidae and Ommatostrephidae. It is more rounded in small specimens, but later becomes cylindrical (Figure 114). The 4 longitudinal and 2 transverse
248 folds of the neck are typical but less developed than in the Ommatostrephidae. On the posterior part of the third longitudinal skin fold is the olfactory tubercle, situated on a lobe. The funnel pit of larger specimens has a distinct edge, without foveola; the lid margin also shows the typical structure, with a sharp sinus.

The arms are of different length according to the formula 3, 2; 4, 1. The two longer lateral pairs are almost of the same length, and so are the shorter median pairs. The arms have a square cross section. The swimming margins are typical but less strongly developed: there is a weak longitudinal fold on the distal part of the first arm and along the outer edge of the whole second arm; the third arm has a narrow, thick margin, and the outer edges of the fourth arm are also narrow. Protective margins are always present, but on the outer side of the fourth arm they are only indistinct edges; elsewhere they have strong supports, as numerous as the suckers in the outer rows. As usual (p. 118), the true supports are fused with the pillars of the suckers nearly their whole length. Only the ends of the supports of the protective margins may project; the stalks of the sucker are situated close to these ends. The V arms bear 4 rows of suckers throughout life. The suckers of the median rows are situated on low pads, each near the base of a distally following pillar of the outer row. The suckers of the median rows are smaller than those of the outer rows. On the other arms the suckers of the median rows are transformed into hooks which are more curved and have longer stalks than those of the Enoploteuthidae and resemble in this respect the hooks of the Belemnitidae and Belemnoteuthidae. The high margin of the sucker rings bears 8–12 rake-shaped teeth.

The tentacles are quite strong. Their stalks bear a typical margin along the rounded outer side, at least distally; the inner surface is delimited by distinct edges which are fused distally with the protective margin of the hand part. The club has a well-developed swimming margin and is generally of typical form (Figure 116).

(249)

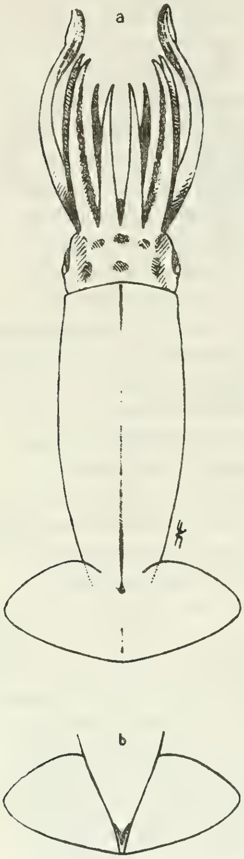

FIGURE 116. Young *Gonatus fabricii* from Bergen, 2×. a) Dorsal view, b) ventral view of posterior end. Figure b shows the cone and adjacent parts of the cone flag, and the projecting, still short apex of the body. The fins are very short, typical in form, (perhaps slightly shrunken). They are already fused in the middle, and the comb of the fin cartilage is visible as a dark line in the posterior part of the dorsal side (p. 227). The fins diverge anteriorly, and the gladius is visible (when the skin is worn) as a dark line extending to the anterior margin of the mantle, although it is indistinct in the middle third. The muscular mantle has already surrounded the gladius, and only the keel of the rhachis is visible. The mantle sac is spindle-shaped, slightly narrower anteriorly. The anterior margin shows the form of the adult animal (see above) The suckers on the arms are quadriserial or still in 2 zigzag rows; the main hook on the club is developing and very large. The swimming margins of the arms are hardly visible at this stage. The buccal funnel consists of 7 parts.

The primary arrangement of suckers is probably as follows: there are 4 regular rows distally which divide into 8 rows near the hand part; the fifth row passes into the main row. The hand part bears more than 8 (probably 16) rows, including a ventromedian row, which is the main row. Many of the adjacent suckers disappear, leaving a bare area. The main row cannot fill this bare area since some of its elements are lost, especially in the proximal part, in which only 5–8 suckers remain. The subdistal sucker becomes markedly enlarged at an early stage, the distal sucker slightly less; the other suckers remain small and become hooks successively, the most proximal sucker last. About 3–4 marginal rows persist on each side of the hand part (a gap may appear only ventrally near the main hooks). The outer rows pass directly into the marginal rows

of the stalk part. Originally, the stalk part probably has 8–16 distal rows, 4 proximal rows and 2 rows (near the base). These rows, however, are not
249 regular; the marginal rows are close together, while the middle rows are separated by larger intervals and later disappear, so that the gap on the hand part continues. A distinct carpal part is absent (if the interval proximal to the end of the main row is not considered as such, which begins already in the hand part, flanked by the marginal rows). The dorsal marginal row of the stalk part is followed by an alternating submarginal row of adhesive knobs which continues on the hand part. In this area about 6 larger knobs alternate with 6 larger marginal suckers to form a simple row. These 6 suckers have strong pillars which push them closer to the middle of the club.

Protective margins are at least indicated on the entire club. They are wider dorsally, distal to the adhesion apparatus of the hand part, and also on the ventral margin of the hand part. The marginal rows of the hand part are displaced to the margin, which is reinforced by the pillars. (There are depressions at the base of the suckers which are contiguous on the hand part, as in the Loliginidae – p. 194.) The supports of the protective margins correspond to the marginal suckers where these are distinct.

The buccal funnel shows the typical points and supports, and 6 buccal pockets. The ventral attachment is internal.

250 The funnel apparatus and mantle cavity resemble those of the Onychoteuthidae. The outer funnel adductors are widely separated. The funnel bonds and the linear mantle bonds are as in the Onychoteuthidae and Enoploteuthidae. The funnel bonds have grooves which disappear posteriorly. The neck bond has a midrib with a thin longitudinal groove; nearby are 2 wide, deep grooves, then again 2 ridges on each side, which widen slightly anteriorly (cf. Figure 205 in the Ommatostrephidae, which show much simpler conditions).

The mantle cavity shows the typical characters of the Oegopsida, but luminous organs are absent. The funnel retractors are bandlike, moderately strong, adjacent to the body. There is a strong, bandlike musculus rectus abdominis. The renal openings form small papillae. A male gonoduct is present only on the left. In ventral view, the narrow gladius is visible only at the end of the cone; the retractors of funnel and head are inserted on the mantle, not on the gladius. Jaws and radula are unknown to me (cf. Verrill, 1881). The radula is stated to have only 5 longitudinal rows (?) and would thus differ from that of all other Decapoda.

β. YOUNG FORMS

I shall describe the early stages elsewhere, if I can obtain material. (Compare the specimen illustrated by Chun, 1911, Plate 30, Figures 2–3.) Chun considers this specimen as a young Brachioteuthis, while Pfeffer (1912, p. 320) places it in the Histioteuthidae as a new genus and species, "Histiochromius" chuni.

An older young stage from Bergen (Figure 116) deserves particular attention as it shows at first glance the typical characters of young Oegopsida (cf. the figures of young Ommatostrephidae and Onychoteuthidae). Only a closer examination of the suckers of the arms and tentacles shows the special characters of the family.

251 *Chapter 11*

FAMILY BATHYTEUTHIDAE
Pfeffer, 1912

Contents: a. Diagnosis. – b. General. – c. Genus Ctenopteryx (p. 252). – d. Ctenopteryx siculus.

a. DIAGNOSIS

Suckers arranged in 4 rows on the arms, in more than 4 rows on the tentacle clubs. Fins subterminal,* either restricted to the posterior end of the body (Bathyteuthis) or extending far anteriorly (Ctenopteryx, Figure 121). Buccal points with small suckers. Gladius with a leaf-shaped flag, an indistinct, flat cone and a very long free rhachis.

b. GENERAL

Pfeffer placed two very different genera in this family, Ctenopteryx and Bathyteuthis and the family is therefore probably not quite natural. These two genera differ sharply from each other and cannot be considered as close relatives. However, they have some special relationships, which are best expressed by placing them in one family. These relationships place both genera into contrast to all other Oegopsida. Ctenopteryx and Bathyteuthis are each represented by only a single species.

The specific characters of the family are partly juvenile characters and partly primitive characters of all Oegopsida. Four of these characters are given below:

1. The form of the gladius, with a long, narrow rhachis (cf. Figures 122 and 106 with Figure 131, etc.) agrees with the general juvenile character. 2. The subterminal position of the fins is also a juvenile character. 3. The occurrence of suckers on the buccal funnel is an entirely primitive character (p. 119). 4. The ancestral form of all Oegopsida is assumed to have quadriserial suckers on the arms and more than 4 rows of suckers on the tentacle clubs.

The Bathyteuthidae show juvenile or systematic-morphologically primary characters also in other respects.

252 The gladius is surrounded incompletely, so that the rhachis is permanently visible through the skin (Figure 121). The fins are articulated and therefore easily displaced (cf. Figure 120, in which the fins are apparently terminal).

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* Fins which are not contiguous at the end but remain distinctly separated.

The neck folds are weakly developed or absent (but cf. Figure 121). The funnel pit is shallow. The olfactory papilla projects distinctly; it is either isolated or connected with a distinct longitudinal neck fold (Figure 121b). The sinus of the eyelid is indistinct.

The suckers of arms and tentacles are very small and uniformly developed. The tentacle clubs are only slightly widened and have rudimentary protective and swimming margins.

The buccal funnel consists normally of 7 parts. In contrast to all other Oegopsida, it bears very small suckers. In Ctenopteryx, there are numerous such suckers in a biserial arrangement, as in Loligo (Figure 77 on p. 179).

The mantle cavity shows the typical relationships. The female gonoduct is paired, but we do not know whether the male gonoduct is paired or single. Noteworthy is the presence of accessory nidamental glands in Ctenopteryx (are such glands absent in Bathyteuthis?). Hectocotylization has not been observed.

On Bathyteuthis see Chun (1911).

c. GENUS CTENOPTERYX Appellöf, 1889

DIAGNOSIS

Fins extending to near the anterior margin of the mantle in postembryonic development and with a characteristic differentiation into transverse, raylike muscle supports and a delicate connecting membrane. A large, flat luminous organ present on the ventral side of eye bulb. Female with accessory nidamental glands which are connected in the middle.

d. CTENOPTERYX SICULUS (Vérany, 1851)
Pfeffer, 1900

LITERATURE

1851 Verany (p. 51, Plate 27), Sepioteuthis sicula.
1889 Appellöf (p. 4, Fig. 1–6), Ctenopteryx fimbriatus.
1894 Joubin (p. 65, Textfig.), Ctenopteryx cyprinoides.
1896 Jatta (p. 118, Plate 31, Fig. 1–10), Calliteuthis neuroptera.
1900 Pfeffer (p. 172), Ctenopteryx siculus (Vérany) Pfeffer.
1900 Joubin (p. 47, Plate 14, Fig. 3–5), Ctenopteryx cyprinoides and (p. 49) fimbriatus.
1903 Lo Bianco (p. 172), Ctenopteryx fimbriatus.
1904 Jatta (p. 221), Ctenopteryx siculus.
1906 Ashworth and Hoyle (p. 2), Ctenopteryx fimbriatus and C. cyprinoides, also (p. 6) Sepioteuthis sicula and Calliteuthis neuroptera (p. 6).
1910 Chun (p. 189, Plate 37, Fig. 9–11), Ctenopteryx siculus.
1912 Pfeffer (p. 332), Ctenopteryx siculus.
1916 Naef (pp. 14, 17), Ctenopteryx siculus.
1921 Naef (p. 537), Ctenopteryx siculus.

I have many young specimens of Ctenopteryx from Naples and Messina, most of them early stages, but no adults. Joubin (1900) and Ashworth and Hoyle (1906) have published rather incomplete descriptions of adults.

253 EARLY JUVENILE FORMS

The youngest stages are easily identified, although my specimens were not particularly well preserved (Figure 116). They are typical larvae of Oegopsida in which the third pair of arms consists of small papillae which are not visible in side view. The fourth pair of arms is smaller than the first and second pairs but resembles them in form. The fins are small and widely separated and resemble those of the next stage, as far as this can be determined from their conserved (shrunken) condition. Particularly characteristic are the tentacles. They are short, thick stalks with characteristically flattened, widened, rounded clubs, with a chromatophore on the outer side. Their inner surface bears about 20 small suckers in more than 4, dense, irregular, longitudinal rows. There are 2 chromatophores on each side of the mantle. Both upper pairs of arms bear a well developed sucker.

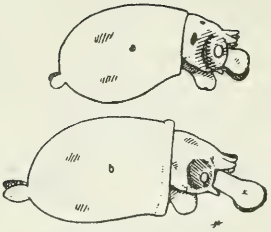

FIGURE 116 [sic.]. Very young larvae of Ctenopteryx siculus, 10×. Preserved specimens from the Messina plankton. Note the formation of fins, arms and tentacles.

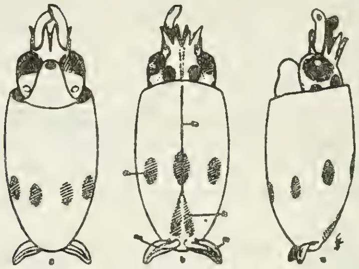

FIGURE 117. Young larva of Ctenopteryx siculus, 7×. Drawn from a living specimen from the Naples plankton (December 1911) and completed after preservation. Note particularly the formation of fins, the insertion of the gladius, the arrangement of the 13 chromatophores (Ch), the formation of the arms and tentacles and the general outline.

Ra — translucent rhachis; Ch — chromatophore; Fa — flag; Mu — muscular support of fin; Ht — membranous part of fin.

These two larvae are representative of a number of similar larvae. The following stage is larger, but does not differ much. Figure 117 shows such a specimen from the Plankton in Naples; the animal was preserved after it was observed alive.

The general habitus is typical for the larvae of Teuthoidea, particularly of the Oegopsida. The insertion of the gladius is distinctly visible on the dorsal side of the narrow, ovoid mantle. The free rhachis is longer than in the adult (Figure 122), and the flag bears a flat, distinct cone posteriorly. Particularly characteristic are the fins. They are normal in general outline, but they are characteristically pointed laterally. They are small and leaf-shaped, supported by a muscular midrib (Mu) with a widened basal part which is attached on the posterior part of the flag of the gladius. There
254 is an equatorial circle of 7 large, brownish yellow chromatophores on the mantle sac.

The 3 typical processes of the mantle margin are still very indistinct; the mediodorsal process is slightly indented, as is often the case (Figure 67 on p. 161). Funnel and head show the normal conditions of such stages. A marked progress is evident in the arms. Both upper pairs of arms are much longer and bear 3–4 suckers in a zigzag arrangement; the ventral arms are only slightly less developed, the LV arms are well developed and bear 2–3 "anlagen" of suckers. The clubs have become longer and have a distinct pointed end; otherwise they resemble the clubs of the preceding stage, which are more contracted because of bad preservation.

INTERMEDIATE JUVENILE FORMS

I show only the fin of a specimen intermediate between the preceding and the next stage (Figure 118d), which shows the transition to the form of the fins of Ctenopteryx. The muscular midrib has become wider together with the fin and begins to sprout new ribs at the anterior end, which are connected at the base with the original midrib. This process continues to the definitive state.

The following stage already closely resembles the adult animal in its
255 habitus but especially in the arm apparatus and fins. The fins have 12 distinct supports, all based on the first support, either in its basal part, which extends along the base, or in the projecting part of the first support. The whole new part of the fin thus appears not as a new formation but as differentiations of the old part. The anterior part of the growing fin is already no longer situated on the gladius, but on the muscular mantle, which later becomes wedged between fins and gladius. This process does not abolish the articulation between fins and their substrate but transfers it to the mantle, as in Loligo and many other Teuthoidea. The fins are not contiguous posteriorly, they are subterminal, but they can be brought into contact by their articulation (Figure 120).

The fin supports are connected by a very delicate membrane. There is a fine undulate line at the margin which is slightly indented between the supports. The insertion of the gladius in the mantle is still unchanged and the flag is clearly visible through the skin. The three typical corners, however, are already distinct on the mantle margin.

(254)

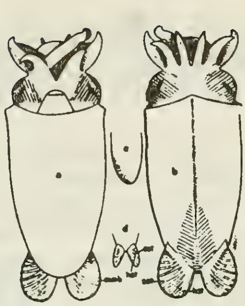

FIGURE 118. Young stage of Ctenopteryx siculus. 5×. c) posterior end of a similar stage with the fin removed, showing the insertion of the gladius in the muscular mantle. d) posterior end of a younger specimen, the fins of which are just beginning to grow, showing the development of new fin supports at the anterior part of the fin base. The main figure shows the continuation of this process: new fin rays develop, at first on the same base, as the fins grow anteriorly along the mantle. Note the formation of the typical mantle margin, of the arms and their protective margins, the eyelid, the insertion of the gladius and its relationship to the fins. (Preserved specimen from the Naples plankton.)

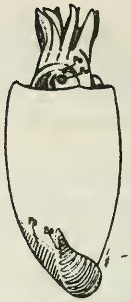

FIGURE 119. Young stage of Ctenopteryx siculus, lateral. 5×. Note the structure and attachment of the fins, the position of the flag of the gladius, the mantle margin, the closed lid margin, the short arms, the upper 3 pairs of which bear distinct swimming margins. (Old alcohol-preserved specimen.)

(256)

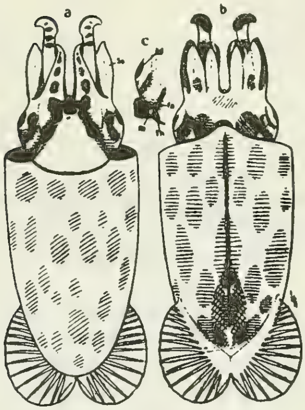

FIGURE 120. Young stage of Ctenopteryx siculus. 5×. Note the general resemblance to Figures 118 and 119 with respect to the fins, gladius, mantle margin, head and arms. The chromatophores, brownish yellow in life, are distinct and present already in the youngest larvae (cf. Figure 116 on p. 253). The small figure shows the olfactory tubercle (Rt) after the funnel and mantle margin have been slightly separated; the tubercle projects markedly and is situated near a small longitudinal fold (Fa).

Th – funnel bond; Ld – primary lid; Ss – swimming margin.

Marked progress is evident in the arm apparatus. They are still very short, but they have already swimming margins. Also the protective margins begin to develop, but supports are not yet recognizable in this or the following stages. The suckers already have a quadriserial arrangement on the distal part of the upper 3 pairs, but there are only 2 rows on the ventral arms. There is only a single row at the base. This condition persists to the adult stage.

The buccal funnel is already developed, consisting normally of 7 parts, but the points are still short and bear no distinct suckers.

Only traces of chromatophores are still recognizable in this specimen and their arrangement apparently resembled that shown in Figure 120.

A similar stage is shown in Figure 119. This specimen resembles the stage described above in all important characters. Whereas the former specimen has a wide open lid with an indistinct sinus, this specimen has a completely contracted primary lid fold which permits only a narrow communication between the eye chamber and the exterior. Such a contraction (here not even maximal) is common in larvae of Oegopsida. The figure shows that the pupil is translucent even in the preserved specimen; in the living animal, the lid fold is completely transparent. This condition occurs as a transient stage in the embryonic development of the Loliginidae (Vol. II, Plate VI, Figure 9).

A perfect picture can be obtained from a slightly older specimen from Messina, preserved in formol (Figure 120). Its habitus still resembles that of the preceding specimen. The fins have 15 rays and resemble those of the preceding stages, but they still have the first formed support. The fins are close together posteriorly, so that they appear fused but they extend
256 further anteriorly on the mantle than the increase of the rays alone would have caused.

The funnel is very strong and the head rounded. The eyes have begun their lateral displacement. The lid is open but rather narrow. The relative length of the arms is 4, 3, 2, 1. The ventral arms are much longer than the third pair, and this is distinctly longer than the second pair. The dorsal arms are markedly the shortest. The tentacle club is further developed and its end longer. The tentacles are strongly contracted because of preservation in formol.

As typical for young Oegopsida, the olfactory organ forms a large projecting papilla and is adjacent to the longitudinal edge of neck on the outside.

The well preserved chromatophores are still regularly arranged and the main chromatophores can be recognized, particularly 3 on the dorsal side of the mantle and 2 on the head. These are already present in the youngest larvae (Figure 116 on p. 253).

OLDER ANIMALS

In July 1914, I obtained in Naples a severely damaged but very interesting, large, young female (Figure 121; the situs of the mantle cavity is shown in Plate III, Figure 4) which showed a number of important facts. In size and development, it resembles Jatta's specimen (1896, Plate 31, Figures 1–10). I used fragments of Jatta's to reconstruct this specimen, the clubs of which were missing.

There are marked differences in the general habitus, particularly in the form of the fins, the larger eyes and the longer arms. Skin and chromatophores are badly preserved.

The muscular mantle has already surrounded the gladius as far as the rhachis, which is visible darkly through the skin. The funnel is detached by the strong contraction of the muscular mantle. Figure 122 shows the shell of this animal (drawn by Merculiano from Jatta's specimen). No

257 terminal cone was shown in the original figure, but it is certainly recognizable in my specimen. The cone is flat, spoonlike, with a low margin, which I have indicated by a slight correction in Merculiano's drawing. A terminal cone has also been described for the large specimen of Joubin. (cf. Figure 62 on p. 146).

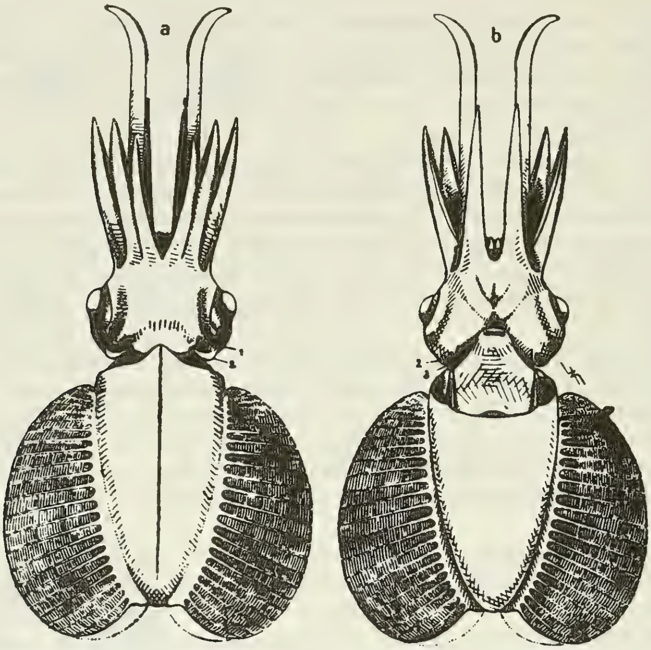

FIGURE 121. Young female of Ctenopteryx siculus. 2×. Reconstructed drawing after a damaged specimen from Naples (July 1914). The fins are spread, the arms are extended, the clubs have been completed after Jatta's specimen. The probably natural outline of the posterior margin of the fins is indicated by a dotted line (cf. also Plate III, Figure 4, which is drawn from the same specimen). Note the form, size and structure of the fins, funnel, funnel bonds, neck folds (1–3), eye lens, eyelids, tentacles and buccal funnel.

The fins are typical, almost at the peak of their development. However, their posterior part is still larger than the anterior, which has not yet reached the anterior margin of the mantle (see dorsal view). It is not certain that the fins ever reach the anterior margin, as a small area remains free on the side of the mantle in all other Teuthoidea with long fins. The outline of the fin has been reconstructed according to the length of the rays. These are usually drawn too narrow, as they appear in preserved material, because preservation causes contraction of the membrane, so that the rays become curled. The fins of the live animal are at least as wide as shown in the figure, perhaps still wider. Their posterior margin is damaged and appears as shown in the drawing. (A dotted line represents the probably natural outline of the fins.) The fins grow anteriorly because new rays are formed at their anterior end, but this growth, cannot be the result of the formation of new rays. If there are 12 rays already present in the stage shown in Figure 120, it appears that these rays occupy a greater part of the mantle length than in the younger stage. We have thus to assume that a further relative increase in length takes place.

258

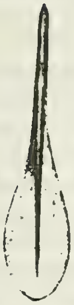

FIGURE 122. Gladius of a young Ctenopteryx siculus, drawn by Merculiano for Jatta (1896). Compare with Plate 30, Figure 4 of his work.

(259)

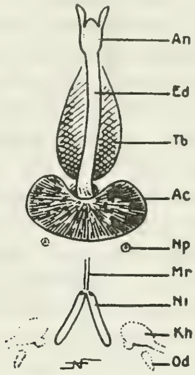

FIGURE 123. "Anlage" of the female genitalia of Ctenopteryx siculus. 6×. Compare with Figures 81, 82 on p. 183 and Figure 4 of Plate IV, especially the "anlage" of the ridges of the accessory nidamental glands, which are not distinct in these figures.

An – anal papilla; Ed – hind intestine; Tb – ink sac; Ac – accessory gland; Np – renal pore; Mr – musculus rectus abdominis; Ni – nidamental gland; Kh – branchial heart; Od – oviduct.

The dorsal corner of the mantle margin projects markedly. This is due more to a contraction of the mantle than to growth of the corner.

The presence of distinct longitudinal neck folds is remarkable, but transverse neck folds are hardly visible. The first, second and third fold of Prototeuthis (Figure 53 on p. 136) can be recognized; the fourth fold is absent, because of the absence of a distinct funnel pit. The third fold was already present in the preceding stage (Figure 120c) and bears the olfactory tubercle in its posterior part; it projects markedly and appears almost stalked. Unfortunately, these places are not quite intact in the preparation.

The funnel is quite typical. It is shorter than in the younger stages and has a simple attachment (cf. Plate III, Figure 4). On the other hand, the eyes have become relatively larger, not only absolutely, and the lenses are very large. This is not surprising since this is a true deep-sea form. The lid fold is slack, so that the lid is wide open and there is a small sinus at its anterior margin. A flat luminous organ occupies a large part of the ventral surface of the bulb.

The arms are of typical length (formula: 4, 3, 2, 1). The ventral arms are now much longer than the others and the dorsal arms shorter. However, all the arms have become much longer than in the preceding stage. (This may be due in part to the better preservation of the specimen, in contrast to the strong contraction caused by formol in the preceding stage.)

The 3 upper pairs of arms have swimming margins which are narrower than in the preceding stage, because the arms are longer. The protective margins are widened, especially on the ventral inner margin of the upper 3 pairs of arms. The margins are more than half as wide as the arm. They are smooth (folded over in the figure), without distinct transverse supports (because the suckers are small). The three upper arms bear proximally 2 rows of suckers (or one zigzag row) and at least 4 rows distally.

The ventral arms have only 1–2 rows or a loose zigzag row of suckers. These are very small, which may be connected with nutrition. The food of this animal probably consists of small plankton.

The tentacles are long, corresponding to the length of the arms (the missing clubs of my specimen were reconstructed after a similar specimen from Jatta). There are no swimming or protective margins on the club. The uniformly small suckers of the club are arranged in more than 8 rows in the middle and in fewer rows in the distal area. The tentacles are shown extended in the drawing; but their base was in fact curved and retracted into the pocket. The pockets of the tentacles are deep and the base of the tentacle stalk can be retracted into them in the form of an S. The attachment is at the upper end of the S-shaped part; the lower end continues in the projecting
259 extended part of the stalk (cf. Sepia). As in Loligo (p. 178), the pockets are situated partly on the median side of the eye bulb and are separated only by a thin membrane from the adjacent orbital cavity (cf. Figure 76 on p. 177). The mouth area shows the typical relationships of the Teuthoidea: there are 7 buccal points of about equal length with biserial suckers, 6 deep buccal pockets and the usual attachments,* of which the ventral ones are attached in the middle, as in Loligo (p. 179) and in the Onychoteuthis-like forms (p. 241).

Opening of the mantle cavity of a young female disclosed a number of characteristic details. I found distinct "anlagen" of the accessory nidamental glands at the same place as in Loligo (Plate II, Figure 2), which are absent in all other Oegopsida (Plate III, Figure 4). Their identification is based on their position and structure. They are situated anterior to the renal pores, and form a well delimited (cf. Figures 81, 82 on p. 183) glandular surface, the epithelium of which forms a dense radial pattern of folds or ridges (cf. Figures 48, 49 on p. 125). Glandular pores are not yet formed between the ridges. This structure differs in two related aspects from the typical "anlage" of the accessory glands: 1) it is unpaired, because the two accessory glands are fused; 2) the ridges radiate not from two centers but from a single center, which is situated in the middle of the anterior margin, so that the ridges form a fanlike figure. The latter point is more important, because a median fusion of the accessory nidamental glands occurs also in the Sepiidae and Sepiolidae, where the glands develop at first separately (p. 125). However, a fusion of the centers of development of the glands is characteristic only for Ctenopteryx. This phenomenon can be better understood if we compare it with the Loliginidae, which resemble Ctenopteryx closely in so many aspects. The centers of the accessory

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* The ventral attachment of Bathyteuthis is external, as in the Ommatostrephidae, Thysanoteuthidae and Enoploteuthidae (cf. Chun, 1910, Plate 25, Figure 3). This is a further reason to doubt the homogeneity of the family. It should be remembered, however, that also in Ctenopteryx the inner side of the arm is so narrow and the connection with the median edge so loose that a displacement is easily possible.

260 nidamental glands of the Loliginidae are situated not in the middle of the "anlagen" but closer to the inner side (see the smaller drawing in Figures 81, 82 on p. 183). The conditions shown there are more advanced, because the radial ridges are only distinct in the marginal zone. However, their absence from a certain point of the inner margin shows the primary condition, i. e. that the ridges radiate from one point at the inner margin. The ridges are rather longitudinal behind this point, so that we obtain an arrangement as in Ctenopteryx in the posterior and lateral parts, if the centers are assumed to be closer together. However, this pattern can only be obtained if the anterior and inner part of the glands is suppressed.

The development of these "anlagen" is unknown. They probably eventually become a weak accessory gland. (Chun did not find such "anlagen" in Bathyteuthis, but he may have overlooked the small rudiment. Traces of such structures may perhaps be found in Gonatus).

There are no other striking characters in the mantle cavity, except perhaps the absence of the posterior pallial veins (Plate III, Figure 4). The vascular supply of the fins has probably passed to the lateral pallial veins, which always have this function in the forms with long fins (Sepia, Sepioteuthis, etc.). The funnel bond is simple, like the mantle bond. Anal papilla, hind intestine, ink sac, funnel retractors, gills, renal papillae, mantle septum are typical in form and position. The vena cava is distinctly displaced laterally; the venous appendages are visible through the large renal sacs.

The juvenile nidamental glands are formed as in Loligo (Figures 81, 82 on p. 183), but their posterior ends diverge. The "anlagen" of the gonoduct are visible behind the branchial hearts: the rounded part, the "anlage" of the oviduct gland, and a longer posterior part, the proximal, coelomic oviduct.

Hectocotylization is unknown in Ctenopteryx. I could not examine jaws and radula.

Specific characters are the form of the fins and pockets of the tentacles, which contain at least a basal part of the tentacles. This is known otherwise only in the Sepiidae. The following characters are typical for the Oegopsida (i. e. primitive): a) the formation of suckers on the buccal points, as in the ancient Sepiidae (S. aculeata) and the Loliginidae; b) the "anlage" of the accessory nidamental glands, which have disappeared in all other Oegopsida (as far as we know; c) the quadriserial arrangement of suckers on the arms and the presence of more than 8 rows on the clubs. Even if we do not accept a closer relationship with other, more or less primitive forms (p. 236), we have to consider Ctenopteryx as the earliest independent branch of the stem of the higher Oegopsida. The close resemblance to the Loliginidae supports this.

261 *Chapter 12*

FAMILY ENOPLOTEUTHIDAE
(Pfeffer, 1900, emend.)*

Contents: a. Diagnosis. — b. Definition of the family. — c. Typical structure of the Enoploteuthidae (p. 263). — d. Variation of the type of Enoploteuthidae (p. 265).

a. DIAGNOSIS

Buccal funnel consisting of 8 parts, its ventral supports with an outer attachment. Gladius with a more or less widened, leaf-shaped flag (but cf. Lycoteuthis, Figure 125); terminal cone without a true rostrum. Fins terminal or subterminal. One ventral arm developing into a hectocotylus (Lycoteuthis?). Clubs of tentacles with 4 rows of suckers, of which some median suckers are converted into hooks, like the greater part of the arm suckers (except in the Lycoteuthinae). A small group of carpal suckers with knobs between them developing as an adhesion apparatus at the base of the tentacle club; stalk part without suckers. Eyeball always with pearl-like luminous organs on the ventral side; other luminous organs often present in the mantle cavity, on the outer skin of the mantle, on head and arms. Radula usually with only simple unicuspid teeth, as in the Sepioidea (q. v.).**

b. DEFINITION OF THE FAMILY

I have defined the Enoploteuthidae Pfeffer, 1900 differently by excluding Octopodoteuthis and related forms (see Chapter 21) but Lycoteuthis and related forms certainly belong to this family in my opinion.

As far as Octopodoteuthis is concerned, a resemblance of habitus is distinct. Closer examination, however, reveals marked differences,
262 especially of the buccal funnel, radula, ophthalmic luminous organs and tentacle club (see Diagnosis). On the other hand, Octopodoteuthis is related to the Onychoteuthidae which will be proved in Chapter 21. By contrast, Lycoteuthis and related forms certainly agree particularly

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* With a different composition.

** Other families of this group (cf. Moroteuthis in Hoyle, 1912, Antarct.) also show a trend to such a simplification, which should be interpreted as growth inhibition. Additional cusps become more or less distinct in the largest and strongest forms (cf. Enoploteuthis leptura in Thiele, 1921, Plate 54, and Pterygioteuthis girardi in Hoyle, 1904), especially in the median row.

with the characteristics of the family, and the slight resemblance to the Onychoteuthidae is not important as it is restricted almost entirely to general characters of the Oegopsida. The gladius of Lycoteuthis (Figure 125) has a reduced flag, like that of Onychoteuthis, but this is not typical for the Lycoteuthinae [see p. 266) or for the Onychoteuthidae (q. v.). This is thus a distinctly atypical similarity (p. 25) or convergence. On the other hand, the buccal funnel, radula and ophthalmic luminous organs of all Lycoteuthinae show the specific characters of the Enoploteuthidae, which therefore appear to be a branch of the stem of Oegopsida.

The following review completes the above remarks and proves that the Lycoteuthinae belong to the Enoploteuthidae and the monotypical difference of this family from the Onychoteuthidae:

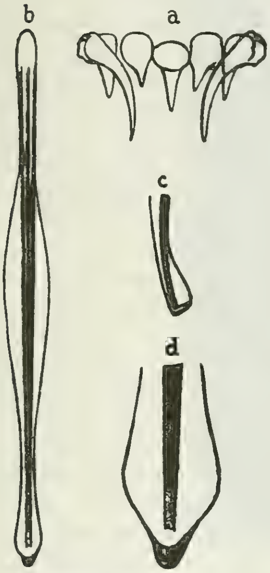

FIGURE 125. Gladius and radula of Lycoteuthis diadema (Chun, 1910, Plate 3, Figures 6, 7, 8, 15). a) Radula, transverse row of teeth (highly magnified).. As is characteristic for all Enoploteuthidae, the 3 median teeth are also unicuspid and simplified, as in the Sepioidea (q.v.) and in contrast to other Teuthoidea (cf. Plates XIV and XV). b) Ventral view of gladius, 2×. The flag parts (lateral plates) are narrow and almost completely reduced, especially in the posterior part. The cone is small but distinct; it is shown in lateral view in c) (optical section) and at a higher magnification in d).

1. The buccal funnel is strongly colored and consists of 8 parts; the ventral supports are attached to the outer side of the ventral arms. 2. The 6 buccal pockets of the 3rd pair are particularly deep ("water pores"; cf. Pyroteuthinae, p. 266). 3. The ventral inner edges of the upper 3 pairs of arms have strong, wide protective margins with sharply projecting supports. 4. The suckers of the club have a uniformly toothed distal margin. The eye bulb bears a ventral row of 5 luminous organs which closely resemble those of the Enoploteuthinae. 6. The distribution of luminous organs in the mantle cavity is the same as in the Pyroteuthinae. 7. The tentacle stalk bears luminous organs, as in the Pyroteuthinae and Thelidioteuthis.

All these characters are typical for the Enoploteuthidae. Most of them are general characters of the family, as the diagnosis shows.

263 c. TYPICAL STRUCTURE OF THE ENOPLOTEUTHIDAE

The characteristic habitus of most Enoploteuthidae is caused by the length of the fins and the relative size of the head. It must be assumed, however, that the ancestral form resembles the general form of Oegopsida more closely, like Lycoteuthis (Figure 110). As in all deep-sea Oegopsida, the body and especially the skin are slightly gelatinous and swollen. The coloration is mainly orange-red, as in most animals of this type (cf. Plate XIX, Figure 9, a related type).

(264)

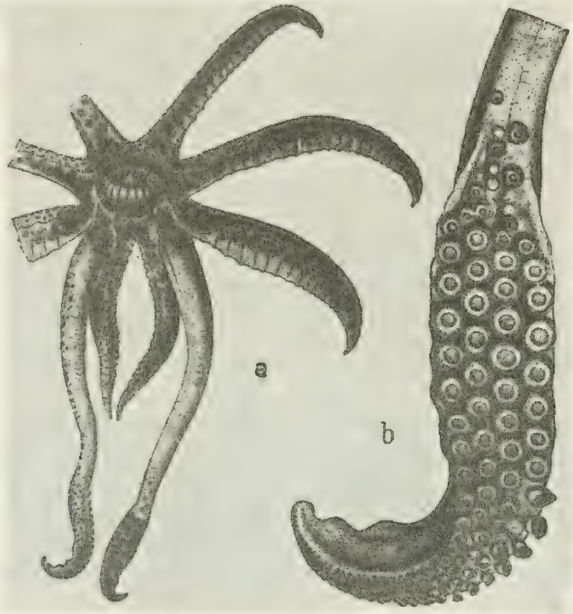

FIGURE 126. Arms (a) and tentacle club (b) of Lycoteuthis diadema, after Chun (1910) (magnified). The drawing of the arms (a) shows the apex of the lower jaw, the inner and outer lips, the buccal funnel with 8 parts, the attachments of which are connected characteristically with the protective margins. The ventral margins of the upper 3 pairs of arms are very large and regular, with distinct transverse supports. The tentacle club (b) bears uniformly toothed suckers in the hand part and the rudimentary carpal part with a few indistinct adhesive knobs. The swimming margin is typical and the protective margins are very weakly developed.

The gladius is as in Loligo but with a distinct, short terminal cone which is spoonlike or conical; the flag (lateral plates) has characteristic lateral corners (cf. Figure 106b on p. 225). The keeled rhachis is still not covered by the muscular mantle in the middle; it is visible as a dark line, while the flag is situated entirely inside the mantle sac. The fins resemble those of the ancestral form of Oegopsida (p. 153), but they are very large and terminal and connected by a fleshy apex which projects distinctly beyond the cone. The neck folds are typical but weakly developed. The funnel pit is weakly delimited, shallow and very wide. The eyelid is also typical, with a weak sinus. The arms are of about equal length (formula: 4, 3, 2, 1). The 3 upper pairs have characteristic swimming margins. The swimming margins of the two dorsal pairs occupy the distal half of the arm; those of the third pair extend proximally beyond the two distal thirds of the arm (Figure 127) and end on the ventral outer edge. All arms bear 2 rows of hooks; suckers are still present at the proximal and distal ends (p. 132). The protective margins have strong muscular supports which originate at the base of the suckers or hooks and are of the same number as the suckers or hooks in the adjacent longitudinal row. There are also "intercalated" supports (cf. Figure 43 on p. 116), associated with the hooks of the more distant row (which have a support on each side).

The tentacle clubs are always very narrow. The inner rows of the hand part are transformed into hooks, except the first and last sucker. The carpal part bears a small group of small suckers with knobs between them (Figure 129). The stalk is bare so that a stalk part is not recognizable in the adult, and the few proximal suckers present at this point in young stages disappear. The protective margins of the club are reduced but are recognizable on the ventral edge of the proximal part.

The buccal funnel is particularly characteristic. There are two adjacent dorsal supports instead of a single support so that the number of rudimentary mouth arms is 8, instead of the 7 present in normal Decapoda. This is a return to a preceding state (pp. 122 and 99) which always appears as a transient stage in the typical development (Vol. II, Plate XXI) and may be inhibited occasionally in a species (cf. p. 244) or in abnormal individuals
264 (cf. Sepia officinalis, Vol. II, Plate XXI, Figure 3); the two dorsal pillars are connected by a narrow membrane, each of which is attached to the dorsal arm.*

The funnel and the situs of the mantle cavity are typical in general. The division of the posterior aorta into 3 main branches at one point is characteristic: one median pallial and two posterior pallial arteries, as in the Loliginidae (Figure 80 on p. 181 and Figure 88 on p. 188), so that the two posterior pallial arteries do not have a common stem as in all other adult Oegopsida (p. 230). However, as such a stem always appears during development,** this is another case of inhibition, especially the complete development observed in the otherwise less specialized Gonatidae and
265 Onychoteuthidae, which are preceding systematic stages of the Enoploteuthidae. The morphological primacy of systematic precedence (p. 19) and complete development (p. 23) is therefore valid for the normal structure of the Oegopsida.

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* These structures appear to be inhibited only insofar as a fusion does not take place. Otherwise they are normal, and it is this which makes them interesting. They demonstrate a "direct division" of a typical "anlage," which becomes functional only when it has become modified. This proves the principle formulated above (p. 34) that ontogenetic transitional forms should be considered as systematic transitional stages even when such stages are unknown.
On the other hand, it must be assumed that such transitional stages persist at least potentially if they appear suddenly in individuals, species or families. Nature proves in this case what may be obtained experimentally in other cases. Such preceding systematic stages can be obtained by the action of external factors and a phylogeneticist would consider them as atavisms (see Vol. II). But this hardly explains the nature of these phenomena. The earlier systematic stages seem to persist in an involute form in the organism, and the systematic morphological variation of our ideal types corresponds to a dynamic-morphological development. The systematic position of an organism also determines its potential character (cf. Concluding Section 2).

** Cf., for example, young stages of the Onychoteuthidae (Figure 149 on p. 308).

In the mantle cavity, the distribution of luminous organs reaches a completeness not known in other Oegopsida: a) one on each side near the anal papilla; b) one luminous organ at the base of each gill; c) 1–3, one of them median, forming a transverse row with the other organs; d) 1–3 in a median longitudinal row on the posterior part of the abdominal complex. In other parts of the body: e) a longitudinal row of 5 organs on the ventral side of each eyeball; f) a few larger organs on the outer side of the tentacle stalk; g) numerous small organs in the skin on the ventral side of mantle, head, funnel and ventral arms, and a few organs on the upper side of mantle, head and arms (see Figures 110, 127 and the list on p. 231).

According to Chun (1911), the organs near the anus of Lycoteuthis emit red light, the median organ between those of the gills and the median organ of the ophthalmic row blue light, and the other organs white light. This is probably the case in other genera (cf. Berry 1920, pp. 156–169).

All these organs are absent in the youngest "larvae," which show the typical characters of early stages of Oegopsida (p. 233). The luminous organs appear gradually and in a strict sequence.

As far as is known for the Enoploteuthidae, hectocotylization consists in a change of the suckers or hooks and of the protective margins of one ventral arm; the margins are widened into lobes, especially on the inner margin, usually only on the distal part of the arm. A male gonoduct is present only on the left side. Accessory nidamental glands are absent.

d. VARIATION OF THE TYPE OF ENOPLOTEUTHIDAE

The variety of forms in the family is evident from the above description of the ancestral form. The Enoploteuthidae are divided into 3 subfamilies. We agree in part with G. Pfeffer's classification (1912), but we include the Lycoteuthinae; the Ancistrochirinae are united with the Enoploteuthinae, but we exclude the Octopodoteuthinae (see p. 261).

REVIEW OF THE SUBFAMILIES

1. Fins rounded, subterminal; cone conical, leaving the apex of the body free. Superficial (cutaneous) luminous organs on mantle, head and arms absent. Nidamental glands present. Oviduct unilateral. Arms with hooks . . . . Subfamily 1: **Pyroteuthinae**
2. Fins rhomboidal - heart-shaped, very large, terminal or subterminal. Cone spoonlike, fleshy apex projecting beyond the cone. Mantle cavity and tentacles without luminous organs. Nidamental glands absent. Oviduct bilateral. Arms with hooks . . . . Subfamily 2: **Enoploteuthinae**

266 3. Fins rhomboidal - heart-shaped, moderately large, terminal. Fleshy apex of body as in the Enoploteuthinae. Hooks absent, toothed suckers present instead. Oviduct bilateral. Nidamental glands present . . . . Subfamily 3: **Lycoteuthinae**

The third subfamily does not occur in Naples. It contains the Pacific genera Lycoteuthis Pfeffer (1910), Nematolampas Berry (1913) and Lampadioteuthis Berry (1916). The author of the last genus established for it a special family (p. 51), though with some hesitation, as he admits. His data, however, show clearly that this genus belongs to the Enoploteuthidae also according to the gladius (p. 56, Figures 12–14), although the cone is very flat.*

The first and second subfamily will be described in greater detail.

SUBFAMILY PYROTEUTHINAE

Pfeffer, 1910

(= **Pterygiomorphae** Chun, 1911)

a) Diagnosis. Fins rounded, leaving the apex free; apex not fleshy but occupied by the cone of the gladius. Suckers converted into hooks at least in the middle of the ventral rows of the upper 3 pairs of arms. Superficial luminous organs on mantle, head and arms absent. Nidamental glands present. Oviduct developed only on one side. Gladius with wide, featherlike flag and a conical cone with distinct rostrum and without fleshy apex. Luminous organs of eye bulb not forming a simple ventral row of 5 but 12–15 in number and irregularly distributed on the ventral and anterior side. Protective margins of 3 upper arm pairs connected at the base between each 2 arms, fused and also fused with the corresponding buccal points. Ventral buccal pockets deeper and surrounding the whole mouth cone like a ring.

The subfamily contains 2 groups of forms, Pterygioteuthis and Pyroteuthis, which are distinguished as follows (in part after Chun, 1910):

1. "A small number of median suckers on the arms are transformed into hooks; this conversion involves only one ventral row or both rows. 267 Tentacle club only with suckers. Left ventral arm hectocotylized." Each eye with 14–15 luminous organs. Oviduct only on right side . . . . **Pterygioteuthis** Fischer, 1896.
2. "Arms with 2 rows of hooks; first, second and third arms with suckers at the end. A limited number of suckers of the ventral median row of the hand part of the club converted into hooks. Right anterior arm hectocotylized." Eyes with 12 luminous organs. Oviduct only on left side . . . . **Pyroteuthis** Hoyle, 1904.

I agree with Chun that these groups are distinct genera, although some of their characteristics are variable. Thus, the left-right hectocotylization varies even in the same species (cf. Illex coindeti; see Pfeffer, 1912, p. 191). It can be said today, however, that the antimeric displacement of the hectocotylization corresponds to the position of the oviduct. This correlation gives greater weight to the character.

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* Joubin (1912) described a related form, Cycloteuthis, which is undoubtedly intermediate between the Enoploteuthidae and Onychoteuthidae. Reminiscent of the former family are its large fins, swollen skin, the form of the apex of the body, the dentition of the suckers and the outline of the gladius. More important characters, however, show that Cycloteuthis belongs to the Onychoteuthidae: the buccal funnel with 7 pillars, the strong rostrum, the tricuspid median teeth of the radula, and the presence of luminous organs on the ink sac, as in Onychoteuthis.

SUBFAMILY ENOPLOTEUTHINAE

(= **Enoplomorphae** Chun)

Diagnosis. Fins very large but typical, with a lateral corner, leaving the fleshy apex of the body free or reaching its end. Gladius flat, with a spoon-shaped cone without rostrum, and a wide, leaf-shaped flag. Middle suckers of arms converted into hooks. Hooks also present in median rows of tentacle clubs; marginal rows absent, at least in part. Scattered luminous tubercles present on mantle, head and arms but not in the mantle cavity. Oviducts developed on both sides. Luminous organs of eye bulb (usually 5) arranged, as far as is known (Thelidioteuthis? Ancistrochirus ?), in a simple longitudinal row, the posterior and anterior organs particularly large. Protective margins of arms not fused with each other or with the buccal funnel. Six buccal pockets present.

This subfamily includes Enoploteuthis Fér. and d'Orb., 1844, Ancistrochirus Gray, 1849, Abralia Gray, 1849, Abraliopsis Joubin, 1896, Thelidioteuthis Pfeffer, 1900. The Mediterranean genera Abralia and Abraliopsis form a narrower group.

ABRALIA-LIKE ENOPLOTEUTHINAE

Diagnosis: Nidamental glands absent. Oviduct glands large, fused in the middle behind the anus (Figure 135). Distal part of spermatophore duct extending to near the anus and almost median in position. Ventral row of 268 suckers absent on hand part of club. Eyeball with a longitudinal row of 5 luminous organs — 3 small between 2 large organs. Ventral side of mantle with numerous small luminous tubercles which form longitudinal rows in some places and often leave a narrow median stripe on the anterior part of the mantle free. Body with large fleshy apex behind the cone. Fins very large, otherwise typical, terminal, i. e. reaching end of apex of body (habitus as in Figure 134).

Enoploteuthis d'Orb. is certainly the most closely related genus; other related forms are Ancistrochirus Gray and Thelidioteuthis Pfeffer as Enoploteuthinae in general. We do not know whether some of the above characters apply to the whole subfamily or only to a larger subgroup. In any case, Abralia and Abraliopsis are particularly closely related. Abralia shows the primary characteristics.

269 *Chapter 13*

GENUS PYROTEUTHIS

Hoyle, 1904

Only one species

PYROTEUTHIS MARGARITIFERA

(Rüppell, 1844) Hoyle, 1904

Contents: a. Diagnosis. — b. Literature. — c. Typical structure of the adult animal (p. 270). — d. Post-embryonic development (p. 275)

a. DIAGNOSIS

Most suckers of the arms converted into hooks, except the smallest apical suckers (which may fall off), some basal suckers, and 4—5 suckers of the ventral median row of the tentacle club. Right ventral arm hectocotylized. Oviduct present only on left side. Luminous organs arranged as follows: 12 on each eyeball (9 larger and 3 smaller), 4 on the outer side of each tentacle (deeply embedded), 10 in the mantle cavity, including one on each side of the hind intestine, 2 on the base of the gill, 3 in a short transverse row between the organs on the gill base, 3 in the continuation of the median line toward the end of the body.

LITERATURE

1844 Rüppell, Enoploteuthis margaritifera.
1849 Gray (p. 48), Enoploteuthis margaritifera.
1851 Vérany (p. 82, Plate 30, Fig.a), Enoploteuthis margaritifera.
1858 Claus, Enoploteuthis margaritifera (p. 262, Plate 10).
1886 Hoyle, Enoploteuthis margaritifera (p. 171, Plate 29, Fig.11).
1889 Carus, Enoploteuthis margaritifera (p. 448).
1894 Joubin, Enoploteuthis margaritifera (p. 62).
1896 Jatta, Enoploteuthis margaritifera (p. 87, Plate 12, Figs.20—32; Figs. 11 and 43).
1899 Joubin, Enoploteuthis margaritifera (p. 69).
1899 Ficalbi, Enoploteuthis margaritifera (p. 81, Fig. 1).
1900 Joubin, Enoploteuthis margaritifera (p. 50).
1900 Pfeffer, Pterygioteuthis margaritifera (p. 166).
1902 Hoyle, Pterygioteuthis margaritifera (p. 1, 6 fig.).
1903 Lo Bianco, Enoploteuthis margaritifera (p. 171).
1904 Hoyle, Pyroteuthis margaritifera.
1904 Jatta, Enoploteuthis margaritifera (p. 200).
1908 Chun, Pyroteuthis margaritifera (p. 187).
1910 Chun, Pyroteuthis margaritifera (p. 136, Plate II, Figs. 1—4).

1912 Pfeffer, Pyroteuthis margaritifera (p. 196, Plate 19, Figs. 17–30).
1912 Pfeffer, Benthoteuthis megalops (Plate 27, Figs. 12–13).
1914 Vivanti, Charybditeuthis maculosa (pp. 55–79, Plate).
1916 Naef (Syst.), Pyroteuthis margaritifera (pp. 15, 17).
1921 Naef (Syst.), Pyroteuthis margaritifera (p. 437).

270 c. TYPICAL STRUCTURE OF THE ADULT ANIMAL

I have only 5 adult males from Messina. The figures are of a larger specimen.

The characteristic habitus of the genus is shown in Figure 127. It resembles the Sepiolidae in the apparent disproportion between head and body (q. v.). This is an extreme even in this family. Muscles strong, skin not swollen but with a strong metallic sheen on arms, head and mantle, with green, red, violet, blue and silvery white tones. The dark chromatophores are bright reddish brown, very large and sparse, another resemblance to the Sepiolidae (cf. colored plate in A. Vivanti, 1914, which is, however, only moderately accurate).

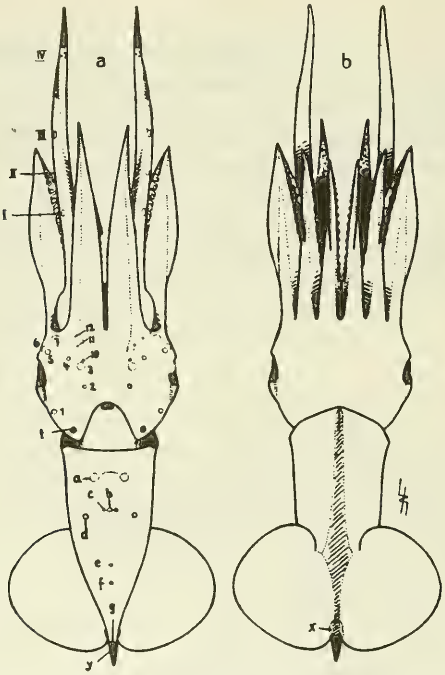

FIGURE 127. Pyroteuthis margaritifera. Adult male from Messina, natural size. The translucent luminous organs of the mantle cavity (a–g) and the eyeball (1–12) are shown in ventral view, which also shows the organs of the tentacle stalks (I–III). Note particularly the form of the posterior end of the body, form of the fins, position of the gladius in the muscular mantle, form of the base and club of the tentacles, and the protective and swimming margins.

y – cone; x – membrane of fin (cf. Figure 65 on p. 153). The coloration resembles that shown in Plate XIX, Figure 9.

Concerning the relations between mantle and shell it should be noted that wearing off of the chromatophores in the adult shows not only the rhachis but also a large part of the flag under the skin (Figure 127b). The mantle thus almost retains its marginal attachment, and the shell is covered only by the shell fold. The fins are therefore still inserted entirely on the gladius and retain the primitive character in being completely separated. The fins approach their typical final form during postembryonic development, forming a blunt lateral corner and a typical "earlobe" at the anterior part of the base. The membranous connection which extends in the juvenile stage (Figure 133) to the posterior end of the body persists as a small membrane
271 (marked with a dotted line near x in the figure) near the posterior part of the base. The muscular rays originate on the relatively short base of the fin and radiate fanwise. The posterior end of the body is lengthened and contains the pointed cone; it widens anteriorly into the small and very short, cup-shaped mantle sac. The mantle margin has a characteristic form, with the 3 typical corners, of which the dorsal is often slightly truncate; the margin is straight between the ventral corners and indented slightly more deeply lateral to them. There is also a blunt, slightly projecting corner on each side of the dorsal margin which is common also in other forms.

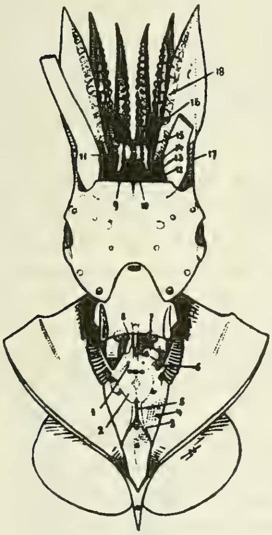

FIGURE 128. Same animal as in Figure 127, after removal of the ventral arms (cut at the base and at the connection with the buccal funnel at 10), mantle cavity opened. Natural size. Note in the arm apparatus: the characteristic base of the tentacle (17); the direct median connection of the ventral protective margins of the third pair of arms (18, 15); above them, the communication between the ventral buccal pockets; laterally, the entrance to the circular canal (9); the cut connection between the ventral buccal pillars and the ventral arms (10) and the preserved connection between the third pillar and the third arm (at 11), the connection between the same pillar (11) and the ventral protective margin of the second arm (16), etc. The mantle cavity contains the 10 luminous organs shown in the preceding figure, i.e. 2 anal (a), 2 branchial (d), 3 interbranchial (b, c), 3 abdominal (e, f, g). Visible on the right are the genital process (7) which projects from the genital pocket; the appendix (6), which is visible through the sinus; Needham's pocket (4) in the upper part of the visceral sac. Typically situated are anus, musculus rectus abdominis, vena cava (8), venous appendages (2), renal papillae (1), branchial hearts and appendages, aorta posterior (5) and its branches, abdominal vein (3), mantle and funnel bonds, etc.

14 – vein of tentacle; 13 – ligament; 12 – perforation (resorbed part) of this ligament.

Neck folds are absent. The funnel pit is distinct, but without a distinct edge. The olfactory organ is a low wart with a transverse indentation. The eyes of this typical deep-sea form are enormous and resemble only those of the Chiroteuthidae and Histioteuthidae. The lid margin has the typical form, with a weakly indicated, shallow sinus.

The arms are short and strong. The ventral arms are the longest (formula: 4, 3, 2, 1). The swimming margins of the third pair extend far proximally; they, and also the protective margins otherwise resemble those of the young stage described on p. 277 (Figure 133). The protective membrane between the fourth and third arms is very low, and there are also traces of the connections between the other arms. There is a characteristic relationship between the bases of (273) the arms and the buccal funnel. This is large, with unusual "bonds" which connect the buccal pillars with the 3 upper pairs of arms for at least a third of their length, so that a system of skin folds is formed which resembles the "inner membrane" of Histioteuthis (q. v.) but it is not the same. 272 (Pfeffer called these structures "sails" (1900 and 1912, p. 189); see also Chun, 1911, p. 113).

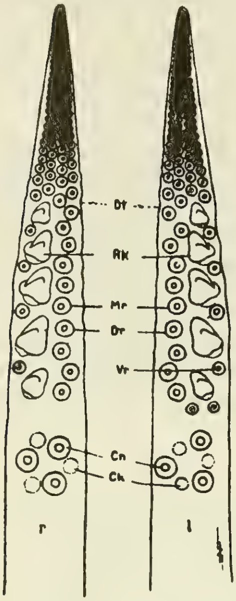

FIGURE 129. Right (r) and left (l) club of Pyroteuthis marg., male. 4.5×:

Dt – boundary between hand and distal parts; Hk – hook; Mr – suckers of median dorsal row, between those of the marginal dorsal row (Dr); Vr – sucker of marginal ventral row; Cn – carpal suckers; Ck – adhesive knobs.

A new character appears in the region of the buccal pockets. The 4 shallower and smaller dorsal pockets are simple slits before the base of the dorsal arms. On the other hand, the 4 lateroventral pockets penetrate deep around the base of the mouth cone, communicate with each other behind the bonds of the ventral buccal pillars (near 10 in Figure 128) and extend (also behind the other bonds) dorsally around the mouth mass, until they meet again in the middle at the base of the dorsal buccal pillar and form another open connection. There is thus a circular tunnel at the root of the buccal membrane, between its outer and inner layers. This tunnel opens at a primary position to the outside, where the LV buccal pockets are normally situated. The ventral protective margins of both LV arms are contiguous at the base of the modified pockets. Another atypical change has taken place at the base of the tentacles, where the perforation (dissolution) of the ligament (near 12 in Figure 128) causes the efferent vein of the tentacle to pass free toward the venous ring of the buccal pocket. The base of the tentacles shows a flasklike swelling already in the juvenile stage (q. v.).

The whole large, characteristically modified buccal funnel is brown violet, and so are also the protective margins and inner surfaces of the arms. This apparatus is apparently markedly extensible in the living animal and probably associated with the capture of prey, which is apparently held by the buccal funnel, leaving the arms free.

The conversion of the suckers of the arms into hooks is almost complete, but normal suckers persist at the usual places. Two such suckers were found at the base of the 3 dorsal pairs of arms in my specimen; there were also numerous small suckers at the ends of the dorsal arms. The apex of the arm is always without suckers (the suckers fall off?), but a few normal suckers may be present there. I found uniserial hooks at the apex of the ventral arms. The hooks still resemble suckers in outline, as they are very short. Their structure, however, is different as even the opening of the sucker at the base of the hook is no longer present (Figures 129, 130).

The clubs are not wider than the stalks of the tentacle, but taper like a whip toward the apex. Swimming margins are absent, protective margins only indicated by the slightly undulate, lateral edge of the hand part. The distal part bears 4 regular rows of smaller suckers. On the hand part the ventral marginal row consists of small suckers; the ventral median row consists of short hooks with their apex pointed obliquely outward. The dorsal median and marginal row have slightly larger suckers and are situated close together so that they almost appear as a double row. The proximal end of the hand part usually bears 1–3 small suckers, usually only on one club.

273 The carpal part consists of 3 adhesive knobs alternating with 3 hooklets in a small group. Dense reddish brown chromatophores make this region appear dark. The edges (protective margins) of the inner side continue on the stalk to near the ligament.

Jatta illustrated an isolated hook (1896, Plate 12, Figure 31; cf. also Vivanti).

The whole funnel part is unusually small (smaller than in the youngest stages, Figure 131). The funnel tube is short and strong, but the funnel bonds have become larger and occupy almost the entire length of the funnel pockets; their form is typical.

The opened mantle cavity (Figure 128) shows that the relationships of the Enoploteuthidae are adapted to the characteristic form of the mantle. A gonoduct is present only on the left side in both sexes. The terminal part of the male gonoduct (7) is situated in a typical genital pocket, the opening of which closes around the base of the duct. The "appendix" (6) does not project freely but is visible through the gonoduct. The spermatophore pocket (4) occupies the left half of the visceral sac.

The female has large nidamental glands which cover a large part of the visceral sac (Vivanti, 1914). These glands occupy the area between the 3 median luminous organs and the nearest median organ behind them; these organs probably become more widely separated in the adult.

(274)

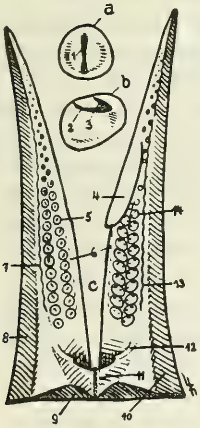

FIGURE 130. Ventral arms of male Pyroteuthis margaritifera. 2×. Cf. Figure 128. The arms are cut off at the base and from the buccal funnel (bond). The left arm is normal, the right hectocotylized. a) isolated hook of normal left arm, highly magnified. b) hook from base of right arm, with 2 ends (2, 3). The middle of the right arm bears a characteristic inwards curved muscular lobe (4).

1 – hook visible through the hood; 2, 3 – ends of the hooks on the hectocotylus; 4 – muscular lobe of hectocotylus; 5 – the sucker shown in a); 6 – rudiments of the median supports of the protective margin; 7 – lateral protective margin; 8 – lateral margin; 9 – cut of arm base; 10 – like 8; 11 – nerves (vessels) of the ventral buccal pillars; 12 – bonds of this; 13 – like 7; 14 – distal (terminal) two-pronged hook.

There are 10 well separated, pearl-like luminous organs in the mantle cavity, 2 very large "anal organs," 2 much smaller branchial, 3 small interbranchial, of which the median is widened into a transverse oval, and 3 small
274 abdominal organs which form a median row in which the anterior organ is situated behind the branching of the posterior aorta, the posterior in the anterior part of the cone. I am not certain whether this organ belongs to the mantle cavity or develops from it because it is situated already in the opening of the cone and is firmly connected with the mantle attached to the cone. It possibly develops from the mantle.

On the ventral side of the eyebulb there are 12 luminous organs which also occupy part of the anterior and dorsal side. These consist of a) 7 ventral organs of different size, more or less distinct, visible also in preserved animals (1–6 and 10 in Figure 127); b) anteriorly, 3 large organs which extend upward (7, 8, 9) and 2 very small organs, covered by the base of the tentacle (11, 12) but also indicated in the figure. All these organs are of a different character and probably emit different light, as in Lycoteuthis (p. 265). As this cannot be determined in preserved animals (cf. p. 276), I shall mention only the visible differences*:

Organ 1 – stalked, directed ventrally, whitish, medium-sized; organ 2 – prominent, overhanging laterally, whitish, medium-sized; organ 3 – flat, lens-shaped, large, lilac; organ 4 – convex, lens-shaped, very small, lilac; organ 5 – reddish brown, lens-shaped; organs 6 and 7 – violet brown, all three of median size; organ 8 – convex, large, lilac; organ 9 – large, strongly convex, lilac; organ 10 – stalked, directed anteriorly, whitish; organs 11 and 12 – lens-shaped, very small, lilac.

The tentacle stalk also bears four luminous organs, as in the Lycoteuthinae (Vivanti, 1914), embedded on the outer side of the stalk. In preserved
275 animals they are hardly visible, ovoid, about 1 mm long. Their position is indicated by a dotted line in Figure 127. The fourth organ is situated opposite the carpal part of the club.

I was unable to examine jaws and radula. According to Jatta, the radula has only simple teeth, as in the Sepioidea (Plate XII, Figure 33).

Figure 130 shows the hectocotylization in Pyroteuthis in comparison with the normal ventral arms. Both arms have a wide lateral margin (8, 10) which is a continuation of the membranous connection with the third arm. Note the attachment to the bucal funnel (12), particularly to the pair of ventral pillars of the funnel, the low, undulate protective margin (7, 13) on the outer side of the hooks, and the small remnants (6) on the median side. The hooks of the left arm are normal to the apex. The condition on the right arm is as follows: 1. The hooks have two prongs, the distal of which corresponds to the normal prong, while the proximal prong is accessory. This applies to the first 19 hooks; the following hooks (about 4) are rudimentary, pressed aside and with only one prong, if they have a point at all. The distal hooks are as on the left arm. 2. The inner edge of the arm (or the otherwise rudimentary protective margin) is transformed from the 8th sucker onwards into a muscular lobe which is curved inwards and ends on the inner edge of the arm.

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* On the fine structure of these organs see Chun (1910, on these organs in Pterygioteuthis) and my remarks in the second part of this monograph. Chun's numbers are placed in parentheses for the homologous organs in Pterygioteuthis (cf. Plate 14, Figure 6): 1 (10), 2 (9), 3 (8), 4 (11), 5 (7), 6 (5), 7 (4), 8 (3), 9 (2), 10 (1), 11 (13), 12 (14). Organs 6, 12 and 15 of Pterygioteuthis are absent in Pyroteuthis.

d. POSTEMBRYONIC DEVELOPMENT

The youngest stage of Pyroteuthis available was drawn while still alive and then preserved. Figure 131a shows the live animal; b) and c) are drawings of the preserved specimen, which is slightly deformed and contracted. This is not the youngest stage, as the LV and V arms are already completely developed, particularly the LV arms, which in this specimen are as long as the DL arms and longer than the D arms. The V arms still retarded, although they later become the longest pair and have the characteristic form of such stages, as they become narrower toward the base. The V arms are connected with the LV arms by a narrow membranous edge which is the "anlage" of the "protective membrane." The arms bear biserial suckers. The protective and swimming margins are only thin edges at this stage. The tentacles are swollen basally, then taper rapidly
276 to small, short, slightly widened clubs with 4 rows of suckers. The mantle sac is short and rounded posteriorly. This is due to the cone, which has the characteristic form of a still deep, spoonlike body. As the dorsal view shows, it passes directly and broadly into the leaf-shaped flag, which occupies about half of the length of the mantle and ends in a narrow, free rhachis. The fins are typically articulated on each side of the flag. The fins of the live animal are rounded lobes, strongly transversely produced and unusually large for such young stages. The fins narrow at the base to a stalklike structure which widens slightly near the insertion. The fins are widely separated in the middle and are thus attached to the marginal parts of the gladius.

The mantle margin shows distinct ventral corners but no dorsal corner. The olfactory organ is still in the larval condition.

All 8 points of the buccal funnel are already developed, but the specific characters of the genus (p. 271) have not yet developed.

The funnel shows the typical characters of such young stages, but funnel and neck bonds are already distinctly developed (Figure 131c). The funnel bonds are still very short and occupy about half of the length of the funnel pockets.

The luminous organs are of particular interest. In the live animal, I found 2 pearl-like pairs of such organs, surrounded by a dark brown margin. One pair is situated near the anus and with a greenish sheen; the other bluish organ is situated on the anterior side of the bulb. Only the preserved larva shows the "anlagen" of two organs on the eyeball behind the already formed organ (b) near the funnel. In the preserved animal, the eyelids (ld) are contracted to a narrow pore over the large lens.

Figure 132 shows an older stage which will not be described since it closely resembles the next stage which is described in detail.

This stage (Figure 133) already resembles closely the adult, except that its posterior end is still little developed.

The gladius is not changed in its basic form but the cone has become more pointed, with a distinct medioventral indentation (cf. Figure 132 as a transitional stage). The cone is not as pointed posteriorly as it appears, because of the presence of a small but distinct fleshy apex. Such a fleshy apex appears as a rudiment also in Pyroteuthis (p. 235). The fins are displaced toward the middle and thus resemble their definitive condition (Figure 127). Their attachment is distinctly subterminal, but a thin membranous fold connects the apex of the body with the median part of their posterior margin. This is noteworthy, since the corresponding part of other young Oegopsida is also strictly membranous (cf. Figures 65 and 189). Reduction of this part could easily cause the formation of a subterminal fin.

(275)

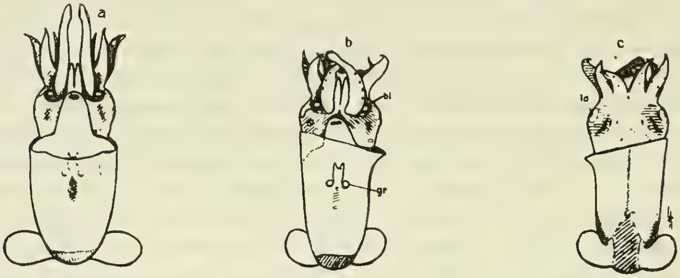
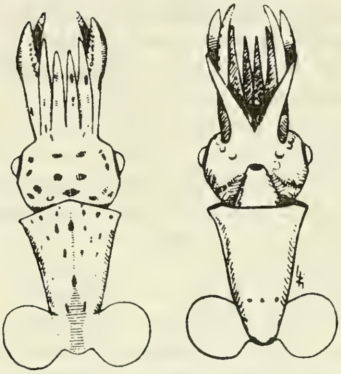
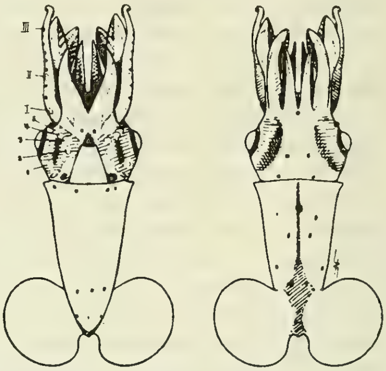


FIGURE 131. Very young larva of Pyroteuthis margaritifera. 8 ×. a) Drawing of a live specimen; b), c) preserved animal. Note particularly the form and insertion of gladius and fins, arm apparatus and luminous organs (bl, gr). The specimen was collected on 23 April 1912 in the Naples ("Amontatura") plankton at 250 m depth).

bl — blue; gr — green luminous organ; ld — orbital pore (primary, contracted eyelid).

(277)





Two young stages of Pyroteuthis margaritifera, drawn after preserved specimens, slightly stylized. 5×.

FIGURE 132. From the deep plankton of the Bay of Naples in May 1914. Note the modification of the form of the mantle; the enlargement of eyes and arms; the widening and median approximation of the fins. Note particularly the olfactory tubercles, the increased number of ophthalmic luminous organs, and the protective and swimming margins of the arms.

FIGURE 133. Specimen from the "Amontatura" plankton at a depth of about 15 m, 2 June 1914:

1—5 — ophthalmic organs (cf. p. 270; Figure 127); I—III — organs of tentacle (ibid.). Characteristic are the general outline, the swimming and protective margins of the arms, and the form of the stalk and club of the tentacles.

The fins are rounded at this stage, still without a lateral corner. A mediodorsal corner of the mantle is also absent, but this depends on contraction.

277 The olfactory tubercle projects as a short cylindrical process. The lid fold of the unusually large eyes shows a weak sinus. However, the most

marked changes have taken place in the arm apparatus. The length formula of the arms is 3, 2, 1=4 at this stage, i. e. the fourth pair has already attained the length of the first. The 3 upper pairs have large swimming margins. These margins are largest on the third pair and smallest on the first pair, but they are still restricted to the distal half of the arm. The ventral arms have a typical protective membrane which continues broadly toward the base of the LV arm, so that an ophthalmic luminous organ is visible in the pocket of the tentacle. Protective margins are present on each side of all arms, particularly strongly on the ventral margins of the upper 3 pairs of arms, their distal part is wide, especially on the DL and LV arms, and has very strong transverse supports the number of which corresponds to that of the suckers in the adjacent row. The proximal part is narrower and firmer, with less distinct supports. The protective margins of both dorsal arm pairs are fused with the adjacent points of the buccal membrane and between themselves, connected by a protective membrane. The DL buccal points connect the D arms indirectly with the DL arms. The LV buccal points are connected with the ventral margins of the DL arms but not with the dorsal margins of the VL arms, which are very low and end free. On the other hand, the normal connection between the LV point with the LV arm is wide and foldlike so that the base of this arm is included in the framework of the "sail." The widened ventral margin of the LV arm also reaches the buccal funnel but more toward the base. The normal connection between the V arms and the V corner extends slightly upward, on the outer side of the
278 point. The ventral buccal pockets are well developed and already quite deep. All 8 buccal points have free ends.

The tentacles extend like whips from a thickened base which bears a well developed ligament. The clubs are small, short, with 4 rows of small suckers.

I have not examined the mantle situs, and have therefore to omit the further development or new development of luminous organs. All 9 larger organs of the eyeball are visible from the outside; the smaller organs are apparently still absent at this stage. The most dorsal organ is visible dorsally (on the left) and certainly shines through during life. The third and seventh organ (counted from the posterior organ) are particularly large already in this stage.

In addition to such larvae, I had only half grown or mature animals. It may be assumed, however, that the conversion of suckers into hooks will soon begin on arms and tentacle clubs. The buccal funnel has still not developed the characteristics of the adult described above, the fins have not yet attained their definitive form, and hectocotylization has not yet taken place in the male.

279

Chapter 14

GENUS ABRALIA

Gray, 1849

DIAGNOSIS

Buccal funnel pale (wine-red). A wide, lobed protective margin on ventral margin of proximal half of club absent. Ventral arms pointed and like a whip at the end, without knoblike swellings (luminous organs). Hectocotylization consisting of a slight change at the distal end of the left ventral arm.

In addition to A. veranyi, this genus contains A. andamanica Goodrich, 1896 (cf. Pfeffer, 1912, p. 137) and A. astrolineata Berry, 1914 (Kermadec, p. 145, Plate X).

ABRALIA VERANYI (Rüppell, 1844) Hoyle, 1909

DIAGNOSIS

Only 4 (3–5) suckers of ventral median rows of tentacle club transformed into hooks; suckers of adjacent ventral marginal row lost. Carpal part of club with 4–5 small suckers and knobs. Fins very large, more than half the length of the posterior body at the base. Luminous organs scattered on ventral side of mantle, not arranged in longitudinal rows, sometimes leaving a narrow free stripe in the anterior part of the mantle.

LITERATURE

1844 Rüppell, Enoploteuthis veranyi.
1849 Gray, Enoploteuthis veranyi (p. 48).
1849 Gray, Enoploteuthis owenii (p. 48).
1849 Gray, Abralia armata (p. 50).
1851 Vérany, Abralia veranyi (p. 83, Plate 30, Fig. b).
1851 Vérany, Abralia owenii (p. 84, Plate 30, Fig. c, d).
1858 Claus, Abralia owenii (p. 261, Plate 10).
1869 Targioni-Tozzetti (2), Abralia owenii (p. 51).
1880 Steenstrup, Abralia veranyi (p. 110, Plate, Fig. 2–6).
1886 Hoyle, Abralia veranyi (p. 38).
1886 Hoyle, Abralia owenii (p. 38).
1889 Carus, Abralia veranyi (p. 448).
1889 Carus, Abralia owenii (p. 448).
1899 Ficalbi, Abralia owenii (p. 82, Fig. 2).

1900 Pfeffer, Abralia armata (p. 167).
1900 Pfeffer, Abralia morisi (p. 188).
1908 Pfeffer, Abralia (Asteroteuthis) veranyi (p. 289).
1909 Hoyle, Abralia veranyi.
1910 Chun, Abralia armata and A. veranyi (p. 79).
1912 Pfeffer, Asteroteuthis veranyi (p. 129); finally corrected to: Abralia veranyi (p. 762, Plate 16, Figs. 1–9).
1916 Naef, Abralia veranyi (p..15).
1921 Naef, Abralia veranyi (p. 537).

280 STRUCTURE OF THE ADULT ANIMAL

Figure 134 shows a leached specimen without a trace of chromatophores. This is a mature female from Nice. The situs of the mantle cavity of this specimen is shown in Figure 135b. We describe below the typical structure of an adult Abralia.

The general habitus strikingly resembles that of the closely related Onychoteuthidae, but this similarity is perhaps not caused by a special relationship but by the possession of generally typical characters or the retention of primary conditions which were assumed for the Oegopsida in general (p. 225) and for the Enoploteuthidae and Onychoteuthidae in particular. A special character of the Enoploteuthidae are the large fins, the total width (span) of which is only slightly less than the dorsal median length of the body and which occupy over two thirds of the mantle length. The lateral corners
281 of the fins extend less anteriorly than in the young specimen in Figure 136, because of secondary growth.

The body has a distinctly calyx-shaped outline caused by the longer and narrower posterior end in comparison with the young stage shown in Figure 136, but the young animal probably had a similar habitus during life. At any rate, the simple conical form of the body of young Abralia-like forms is due at least in part to the reflectory retraction of the head during preservation and to the contraction of the mantle itself. The form of the gladius is shown in Figure 106b. It is inserted as in the young animal (Figure 136). The rhachis is visible in the median dorsal line, while the fleshy apex has become relatively smaller. The mantle margin shows the 3 typical corners, the dorsal is widened and slightly indented. The neck folds and the marginal edge of the funnel pit are weakly developed. The small longitudinal fold which bears the olfactory organ is distinct. The funnel adductors are distinct in the funnel pit. The transversely oval lid fold is widely open, with an indistinct sinus.

The specimen which was preserved in a relaxed state has very long, whip-like arms. The first pair is shorter than the others, which are almost of equal length. True swimming margins are present on the 3 upper pairs, especially well developed on the third pair. The margin is a narrow, indistict edge in the proximal third of the 3rd arm; it then widens abruptly (folded over in the figure) and tapers toward the distal end. The margins of the two upper pairs are narrow, especially narrow on the first pair and only in the distal half. All arms have two protective margins and their supports correspond to the number of hooks or suckers in the adjacent row.

The margins project slightly at the point of the supports. The ventral margins are wider on the second and third pair. The dorsal margins of the first and second pair are connected at the base with the first and second buccal attachment. All arms bear 2 loose rows of hooks (or a single, zigzag-shaped row) except in the distal quarter. They are absent in the proximal (280) fifth of the arms. There are usually 17 (16–18) hooks on the dorsal pairs. They are followed by two rows with about 20 suckers, which decrease rapidly in size; further distally are quadriserial, very small suckers on the whiplike end of the arm (cf. Gonatus). Such quadriserial end parts are absent on the ventral arms. The larger suckers bear 5–7 long teeth at the distal margin; the smaller distal suckers have more numerous teeth.

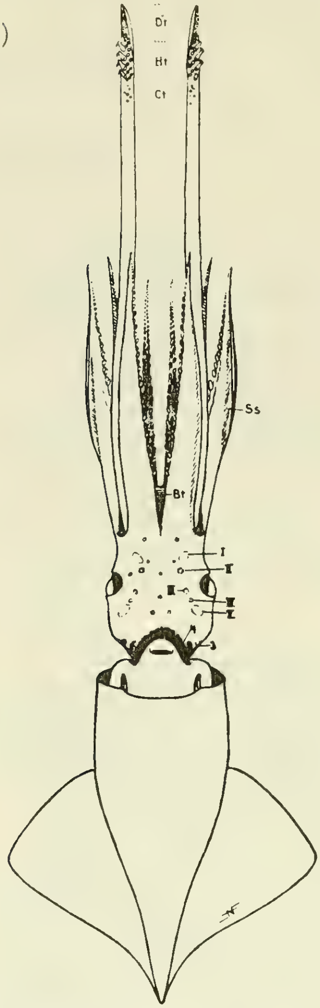


FIGURE 134. Abralia veranyi. Fully grown, mature female from Nice, natural size. Note the general habitus, the luminous organs on the eyeball (I–V), neck folds (3, 4), funnel pit and funnel adductors, swimming margins (Ss), and structure of clubs.

Ct – carpal part; Ht – hand part; Dt – distal part; Bt – buccal funnel.

The tentacles are longer than the body behind them. The clubs are only slightly widened; the protective margins are more distinct dorsally, narrow and less marked on the ventral side. The carpal part bears a group of 4–5 suckers and 4–5 or more knobs. Four (3–5) suckers of the ventral median row on the hand part are converted into hooks; the ventral marginal row is absent, the two other rows consist of medium-sized suckers with teeth all around. The distal part bears 4 rows of very small suckers. The second hook is usually the largest, the first the smallest.

282 The buccal funnel has 8 points, supports and bonds and the 6 pockets typical for the Enoploteuthidae. The dorsal supports are connected at the base with the inner protective margins of the dorsal arms, the following supports with those of the DL arms. The attachment of the LV points ends on the inner side of the LV arms between their protective margins. The ventral supports are connected with the outer protective margins of the ventral arms. Protective margins are also present on the bare base of the arms without suckers, but without supports so that the typical condition for the atypical structures of the Pyroteuthinae exists (see p. 272).

The funnel apparatus, funnel cartilage and mantle cartilage are typical.

Only the largest of the superficial luminous organs, i. e. those regularly distributed on the head, are shown. The smaller organs are distributed as in the young animal (p. 284). A narrow stripe on the median line of the mantle is often without luminous tubercles. This character is usual but not general in Abraliopsis but it appears here only in a small minority of specimens.

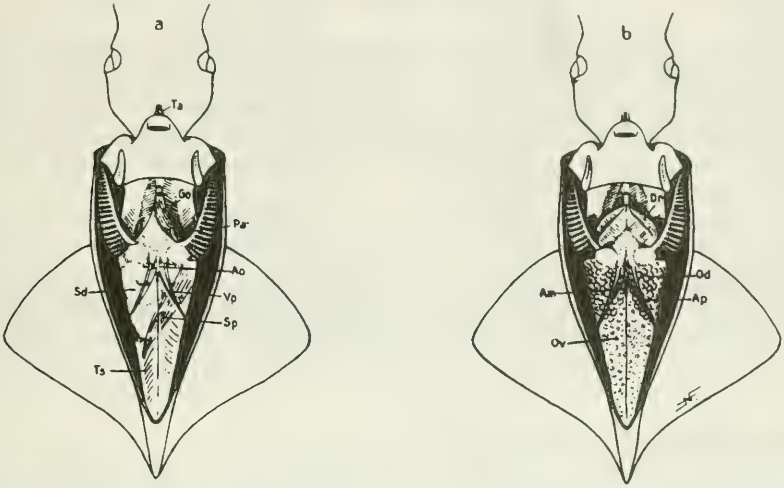


FIGURE 135. Abralia veranyi. Situs of mantle cavity of a male (a) and a female (b), natural size. The female is the same specimen as in Figure 134. The characters of the male are placed in the same outline from a badly preserved specimen. Note the general resemblance to Figure 128 and particularly the branching of the posterior aorta (Ao), which resembles that in the Loliginidae, Sepioidea (Figure 80 on p. 181) and the youngest stages of other Oegopsida (Figure 149), the median and anterior displacement of the distal parts of the gonoduct (Dr, Go), and the large development and median fusion of the oviduct glands (Dr). Also shown are funnel cartilage, branchial hearts, appendix (Pa) of the male, the filled upper parts of the gonoducts (Sp, Od).

Sd — spermatophore gland; Ts — testis; Vp — posterior pallial vein; Ta — funnel adductors; Am — median pallial artery; Ov — ovary; Ap — posterior pallial artery.

Figure 134 shows also the arrangement of the large translucent luminous
organs on the eyebulb. The anterior of the two largest organs is situated
rather deep and is directed anteriorly and inward; the posterior is larger,
283 superficial, ventral, and directed slightly outward. Both are oval. Between
them are situated 3 smaller organs at different intervals, the posterior
almost adjacent to the largest organ, the anterior nearer to the large anterior
organ, the median between the other two but closer to the posterior. The
orbital "window" is situated above the median organ.

The mantle cavity shows the typical topography of Enoploteuthidae with the special development of the genitalia of the Abralia-like Enoploteuthinae. Luminous organs are absent. Figure 135a and b shows the important characters. Gills, funnel retractors, anal papillae, branchial hearts and posterior pallial veins are typical for all Decapoda or Dibranchiata, but the simple trifurcation of the posterior aorta is a typical character of the Enoploteuthidae (cf. p. 264). Particularly interesting is the structure of the genitalia. The oviduct glands (Dr) of the female (b) are enormously developed; they occupy the whole projecting part of the oviduct and appear at first glance as nidamental glands, the function of which they probably fulfill. Like the nidamental glands, the oviduct glands are contiguous in the middle behind the anus (cf. Figure 35 on p. 105); their slitlike opening is directed upwards and anteriorly and therefore not directly visible. The oviducts are visible behind the branchial hearts in the form of a sac filled with eggs.

The male genital duct (a) is displaced anteriorly and toward the middle in its distal part (Go), like the corresponding part in the female, but it is present only on the left side. It is situated in the middle behind the anus, but it originates in the pocket of the gill base, like the appendix (Pa). The entrance to the genital pocket is situated in the pocket of the gill base; it is wide open, as in all Oegopsida.

Hectocotylization affects only the apex of the left ventral arm. It is without suckers and hooks but has widened protective margins which form lobed folds and taper apically. The modification affects about one fifth of the length of the arm on the inner edge, slightly less on the outer edge. The inner lobe is apparently homologous to that of Pyroteuthis (Figure 130).

POSTEMBRYONIC DEVELOPMENT

I do not know early stages of Abralia;* a larva which I considered at first to belong to Abralia belongs to Thelidioteuthis (Figure 143). Figure 136 shows a well preserved, half-grown specimen of the collection of the Zoological Station. It already shows the typical habitus of the genus, but could easily be considered as an Abraliopsis. This resemblance is caused by the pointed conical posterior end of the body, which more closely resembles the typical form in adult Oegopsida, and the disproportionally wide head, which is retracted into the mantle cavity because of preservation in formol.

284 The gladius is completely surrounded by the muscular mantle so that only the rhachis is visible through the skin on the dorsal side. The rhachis is not visible in about the posterior quarter of the dorsal median line, where fins and fleshy apex are contiguous. Because of its transparent, gelatinous consistence, the apex is also visible through the skin as a dark median stripe. Its large size is clearly visible on the ventral side. The fleshy apex is situated not only on the cone but on the entire posterior part of the mantle sac and was erroneously assumed to be part of it. The fins are typical but already very large. Their base occupies over half of the dorsal median line of the body; the length of the fins occupies about two thirds of this line, and their width is nearly equal to the mantle length. The fins are produced posteriorly into a distinct apex. The mantle margin has 3 weak but distinct corners.

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* Such young organisms, however, have been described by Joubin: his "Abraliopsis" juv. (1920, Plate 12, Figure 13) shows no trace of terminal organs on the ventral arms, although it is at least one quarter larger than the specimen shown in Figure 141.

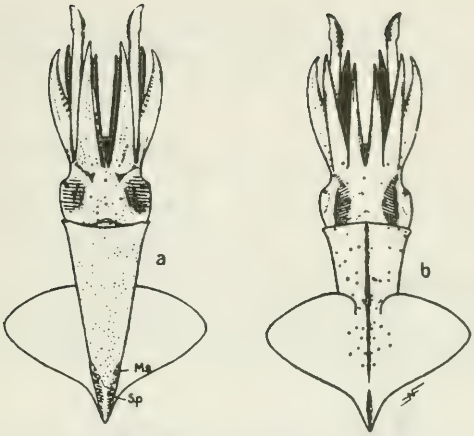

FIGURE 136. Abralia veranyi. Young specimen collected in Naples on 25 October 1908. No. 70 of the Zoological Station. Natural size, slightly diagrammatic. Note the general proportions, the attachment of the (darker) apex of the body (Sp) to the mantle sac (Ms), form of fins and mantle, the contracted primary eyelid, structure of arms and clubs, and the distribution of luminous tubercles (indicated as dots and rings).

The primary eyelid is contracted to a transverse slit, as is often the case in typical Oegopsida; a sinus is not recognizable.

Buccal funnel and arm apparatus resemble those of the adult.

The whole body is covered with superficial luminous organs. They are especially densely and uniformly distributed on the ventral side of the mantle; a free median stripe is not noticeable. The distribution is similar on the ventral side of the head, but the organs are larger and symmetrically distributed.

A row of luminous tubercles is situated at the lid margin; 3 longitudinal rows extend along the ventral arms, and also a number of scattered organs, especially on the base of these arms. On the dorsal side there are luminous tubercles between the fins, on the base of the fins, on the anterior part of the mantle, on the head and on the bases of the DL and VL arms. The dorsal organs, however, are more sparsely distributed than on the ventral side. The 5 large luminous organs of the eyeball are present, but they are not visible from the outside (Figure 134).

285
Chapter 15

GENUS ABRALIOPSIS
Joubin, 1896

DIAGNOSIS

Buccal funnel dark (brown violet). Proximal half of tentacle clubs with lobed ventral protective margin. Apex of ventral arms with multiple, knob-like swellings (luminous organs). Hectocotylization affecting the entire left ventral arm, especially its inner protective margin, which is strongly colored and widened. Tentacle clubs with both marginal rows of hand part suppressed; at least some suckers of median rows transformed into hooks.

In addition to A. morrisi (Vérany, 1837) Pfeffer, 1900, this genus contains A. scintillans Berry, which resembles A. morrisi in all these characters. The generic name of this form, Watasenia (Ishikawa, 1914), is therefore not valid.

ABRALIOPSIS MORRISI (Vérany, 1837) Pfeffer, 1900

DIAGNOSIS

Ventral median row of tentacle clubs with 4 or 5 larger prehensile hooks; dorsal row with 4 or 5 smaller adhesive hooks (typical rotating hooks – p. 132). Carpal part of club with 4 or 5 suckers or knobs.

LITERATURE

1837 Vérany (I), Onychoteuthis morrisii (p. 100, Plate 2a).
1839 D'Orbigny, Enoploteuthis morrisii (p. 338).
1849 Gray, Abralia morrisii (p. 50).
1884 Pfeffer, Enoploteuthis hoylei (p. 17, Plate III).
1886 Hoyle, Abralia morrisii (p. 38).
1896 Joubin, Abraliopsis pfefferi (pp. 9–35, Figs. 1–10).
1896 Joubin, Abraliopsis hoylei (p. 33).
1896 Goodrich, Abralia lineata (p. 10, Plate III, Fig. 46–50).
1900 Pfeffer, Abraliopsis morrisi (p. 168).
1904 Hoyle, Abraliopsis hoylei (pp. 36, 58–64, Plates VIII, X).
1910 Chun, (9) Abraliopsis morrisii (pp. 78, 103, Plates V–X).
1912 Pfeffer, (9) Abralia morrisi (p. 168).

1912 Pfeffer, Abralia pfefferi (pp. 156–160).
1912 Pfeffer, Abralia corrected: Abraliopsis pfefferi (p. 764).
1916 Naef, Abraliopsis morrisi (p. 16).
1921 Naef, Abraliopsis morrisi (p. 537).

The following juvenile forms belong here:

1896 Jatta, Teleoteuthis caribaea (pp. 100–102, Plate XIII).
1900 Pfeffer, Micrabralia lineata (p. 167).
1900 Pfeffer, Compsoteuthis lönnbergi (p. 167).
1908 Issel, Abraliopsis juv. (p. 210, Plate IX).
1912 Pfeffer, (9) Abralia (Nepioteuthion) mediterranea (p. 149, Plate 15, (Figs. 5–7).
1912 Pfeffer, Abralia (Compsoteuthis) jattai (p. 150).
1912 Pfeffer, Abralia (Compsoteuthis) lönnbergi (p. 151, Plate 17, Figs. 10–15).
1912 Pfeffer, Abralia (Nepioteuthion) lönnbergi (p. 150, Plate 15, Figs. 1–4).

286 STRUCTURE OF THE ADULT ANIMAL

The general habitus resembles that of a half-grown Abralia (Figure 136). Preserved specimens have a conical mantle sac with a slight swelling in the middle (p. 282). The gladius shows the typical form of the Enoploteuthinae; it closely resembles that of Abralia but it is not surrounded as far by the muscular mantle. In Abralia, only the rhachis is visible through the dorsomedian skin while here a part of the middle of the flag is also visible, which is covered only by the shell fold. This character may be only of relative value, because the possible median displacement of the fins may temporarily cover the gladius still further.

The fins are very large, their span markedly larger than the dorsal length of the mantle. The fins occupy about three quarters to four fifths of the dorsal length of the mantle, their length at the base to three fifths of its dorsal length.

The funnel pit is shallow, wide, with a distinct margin. Especially distinct are its lateral corners, but they do not form a longitudinal neck fold (cf. Loligo, Plate II, Figure 1, and Ommatostrephes, Plate VI, Figure 1). The three upper longitudinal folds of the neck, however, are distinct; the third fold bears the olfactory organ which is not situated at the base but on a pillarlike support of a short fold. (If the other weakly developed parts of the fold were absent, this would be a strongly projecting or stalked olfactory tubercle.) The anterior transverse fold of the neck is also distinct. The lid opening is wide, with a weakly indicated sinus anteriorly, more or less straight and transverse posteriorly. The lens is very large, like the eye itself.

287 The ventral arms are the longest, longer than the lateral pairs. The dorsal arms are shorter, almost as long as the lateral pairs. The 3 upper arm pairs have swimming margins, which are only indicated in the young stages (p. 291). These margins occupy about half of the length of the first and second pairs; on the third pair they extend to the base, only as a low edge proximally (cf. Figure 134).

The protective margins of the arms show the characters described above, particularly the large ventral margins of the second and third pair. The number of supports is double the usual, i. e. each margin has as many supports as there are suckers or hooks in the corresponding part of the arm. Supports also correspond to the hooks of the zigzag row, as was assumed for the ancestral form of the Decapoda (Figure 43 on p. 116).

(286)

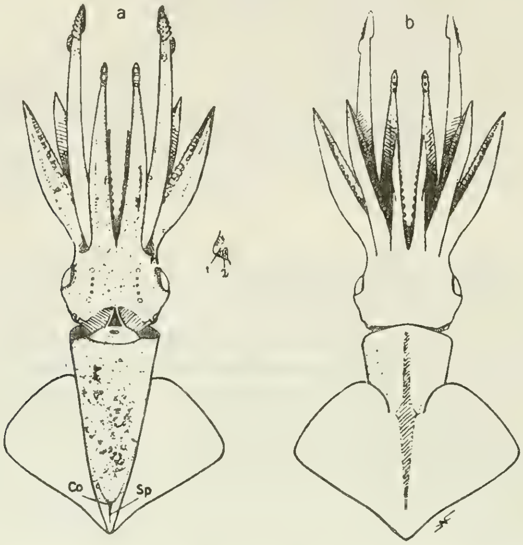

FIGURE 137. Almost adult female of Abraliopsis morrisi. Natural size; after a specimen from Naples, a) ventral, b) dorsal. The habitus resembles that of Abralia (Figure 134), but the gladius is more distinct. The figure shows the structure of the posterior end, the distribution of luminous organs on head and mantle, funnel pit, funnel adductors, neck folds, structure of tentacles and arms (especially the protective and swimming margins), terminal swellings of the ventral arms.

Co — conus of gladius; behind the cone is the fleshy apex with a central supporting cord (Sp) which occupies the position of the rostrum (Figure 157 on p. 319). The smaller figure shows the third longitudinal neck fold (2) with a muscular pillar (1) which bears the olfactory tubercle. The dots (luminous organs) in "a" should be distributed uniformly on the mantle.

Particularly characteristic are the tentacle clubs (Figure 138). They bear a carpal group of 4 or 5 suckers and between them at least the same number of strongly pigmented knobs. Then follows a bare area, followed by the hand part with 5 (4—5) large, wide, prehensile hooks corresponding to the ventral median row, and 4 (4—5) small adhesive (rotating) hooks which correspond to the dorsal median row. The ventral marginal row is absent, the dorsal row consists of very small suckers. There is a short distal part with 4 rows of small suckers and a typical end part which is curved inward.

The hand part varies markedly. Instead of the small hook shown in Figure 138 there may be a small sucker (8) near the last large hook. One or both rows may consist of only 4 hooks. One of the first hooks may also be replaced by a sucker. We observed the following pattern in four specimens (A—D):

Tentacle club	left	right
Large hooks	5 5 4 4	5 4 5 5
Small hooks	5 4 5 4	5 5 5 5
Specimen	A B C D	A B C D

A broad swimming margin extends along the distal half of the hand part and the whole distal part. In all species (also in A. scintillans (Berry)) the ventral edge of the inner surface bears a similar lobe which extends from the base of the carpal group to the second large hook. This lobe is a modified part of the otherwise indistinct protective margin. According to Pfeffer (p. 131, Plate 16, Figure 8), a trace of such a margin is present in Abralia veranyi; I did not find it in any specimens of Abralia and consider it as specific for the genus Abraliopsis, at least in such a degree of development.

The mantle cavity of Abraliopsis shows more or less the same relationships as in Abralia (see Chun, Plate IX, Figures 1–5). Luminous organs are absent in it.

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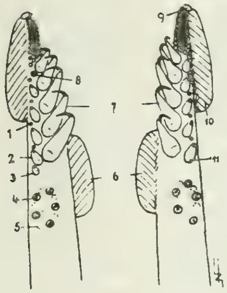

FIGURE 138. Tentacle clubs of the specimen of Figure 137, higher magnification. Note the swimming margins (10), protective margins (6), structure of arms, arrangement of the small (2, 3, 11) and large (7) hooks, carpal group (4, 5) and the inward curved end part (9):

8 – sucker of the row of small hooks but probably undeveloped because of the presence of an accessory proximal sucker (3); 4 – suckers; 5 – knobs of carpal part.

The luminous organs of the mantle are still often arranged in longitudinal rows also in older specimens, but this pattern is markedly obliterated by scattered organs (exaggerated in Figure 137). A median stripe without luminous organs and associated chromatophores extends between the previous inner longitudinal rows (Figure 141) in the anterior part of the mantle or its whole length. This is distinct in good preparations but is not absolutely constant. The projecting part of the funnel bears numerous luminous organs with an increasingly irregular arrangement. At least the largest and first developed (p. 291) organs on the head can be homologized with certainty because they retain their position. Also the later developed organs have a more or less regular arrangement. The ventral arms bear a number of scattered organs mainly at the base and 2 irregular longitudinal rows of luminous tubercles, one median and one lateral. A row of luminous organs originating in the area of the eye sinus extends below the swimming margin of the 3rd arm. Scattered luminous organs are also present on the lateral and dorsal sides of the mantle (Figure 137); I could not find luminous organs on the upper side of the head.

The apical swellings of the ventral arms appear like a string of pearls, with 3 rounded luminous organs enveloped by dark chromatophores; the median organ is the largest (Figure 137).*

There are 5 ophthalmic organs. A later formed organ has appeared behind the anterior organ, which is large in the young stages (Plate IV, Figure 2). The ophthalmic organs emit reddish light.

I have not examined mature, hectocotylized males. The reader is referred to Chun (1910, pp. 82–83), although I am not quite certain that his material belongs to the same species as my specimens from Naples and Messina. (The club has only 5–7 hooks in Chun's specimens, 8–10 in mine.)

289 POSTEMBRYONIC DEVELOPMENT

Nishikawa described several embryonic stages of Abraliopsis and an early postembryonic stage which probably belongs to Abraliopsis scintillans. Pfeffer (1912, p. 149) used the name Nepioteuthion for such early stages. Figure 139 shows a "Nepioteuthion stage" of Abraliopsis morrisi, from the plankton in Messina. It shows the general characters of a young larva of Teuthoidea or Metateuthoidea, as shown by comparison with Figures 1–3 in Plate I. It can be recognized as a larva of Oegopsida by the open eyes, the girdle of chromatophores on the mantle (Figures 116, 117 on p. 253), the stumpy, retarded ventral arms, the stronger third pair of arms (which are still less developed than the second pair), and the still biserial arrangement of suckers on the tentacle clubs (these suckers are quadriserial in freshly hatched Loliginidae). A special character of the larvae of Enoploteuthidae is the relatively early development of the third arms which are more retarded for a longer time in other Oegopsida.

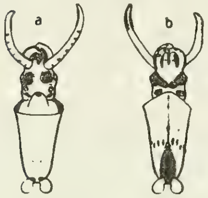

FIGURE 139. Youngest stage of postembryonic development of Abraliopsis morrisi from the Messina plankton ("Nepioteuthion"). 5×. Note the form of fins and mantle, the darkly translucent gladius, the typical form of funnel and head, the arm apparatus and the distribution of chromatophores.

It is not certain that the larva belongs to Abraliopsis morrisi. Other Abralia-like Enoploteuthinae probably pass through very similar stages. This applies also to Abralia veranyi, which is less common in Messina. The present specimen, however, resembles the older and clearly identifiable forms so closely that its position in this species may be considered as certain. Compare, for example, the distribution of chromatophores on mantle and head with that of the following stage (Figure 140). Abralia is also much less common.

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* I could not study their function in the living animal. According to the observations of Watasé, Sasaki and Ishikawa, the apical organs of the arms of the closely related Japanese species A. scintillans are particularly bright and emit a greenish blue to bluish purple light. Their dark envelope (chromatophores) can be opened and closed suddenly. The cutaneous organs emit a pale blue and the ophthalmic organs white light.

The gladius has the typical juvenile form of Oegopsida (Figures 132, 133). It ends posteriorly in a flat cone and is not yet surrounded by the muscular mantle, which is still attached only at the margin. The mantle sac is rounded posteriorly, and the fins form rounded lobes with a narrower base. The fins are connected posteriorly by a distinct transverse edge which occurs also in other young Metateuthoidea and is reinforced during embryonic life by the transverse part of Hoyle's organ (cf. Vol. II, Plate VII; also Figure 88). The fins are otherwise completely separated in the middle. The mantle sac is still without ventral corners, and there are no distinct adhesion
290 surfaces (funnel bonds) on the funnel. The head shows the typical form of early larvae (Figure 88) and the olfactory organ is also situated in its typical position as a flat, low, oval papilla. The arms are of different length, the ventral arms the shortest. The third pair is already as long as the first, but not as long as the second pair. The tentacles are the longest and their distal third bears 2 rows of small suckers. Each arm bears a zigzag row of suckers. Luminous organs are absent.

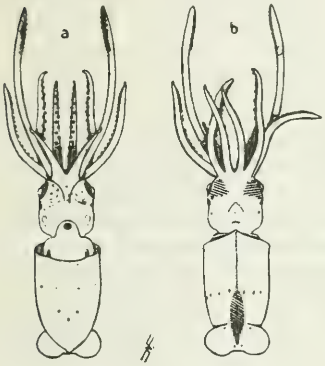

FIGURE 140. Young stage of Abraliopsis morrisi from the Naples plankton, collected on 9 September 1910. 5×. Numerous similar specimens from Naples and Messina are available, but not so well preserved. The specimen was drawn after preservation. Note the form of mantle and fins, translucent gladius, funnel apparatus, head, arm apparatus, chromatophores and especially the "anlagen" of the olfactory and luminous organs (dotted rings).

Compared with this young larva, the following stage (Figure 140) represents a distinct progress. Head and body still resemble those of a young Loligo, i. e. the typical young forms of the Metateuthoidea. The arms, however, are much longer, which is characteristic for the larvae of the Enoploteuthinae and differs from those of the Loliginidae (but compare the young Histioteuthidae as in Figure 175). One unexperienced in the determination of such larvae might believe that the Oegopsida can be distinguished easily from the Loliginidae and related forms by the eyelids. This is not so, because the primary lid fold is very contractile and delicate, and its opening often unrecognizable.

Comparison of the dorsal views in Figures 139 – 141 shows that the mantle has begun to surround the flag; the lanceola appears increasingly smaller. The fins advance anteriorly and towards the middle as their base becomes longer. The transverse edge which connects the two fins at the posterior margin is still distinct at this stage, although it is not connected directly with the cone at the posterior end of the mantle sac but with the very weak but distinct "anlage" of the fleshy apex (Figure 140a).

The mantle margin shows the 3 typical corners, of which the dorsal appears unnaturally large because of contraction of the mantle. The funnel apparatus is typical, with distinct funnel and neck bonds. The head is still of the habitus of an early larva; eyes and olfactory organ are in their typical position.

Of particular importance for the identification of young Enoploteuthidae
is the arm apparatus. The ventral arms are still in the typical stage of
291 inhibition. All other pairs are very long. The first pair is the shortest,
already surpassed by the third pair; the second pair is still the longest.
All arms have a zigzag row of suckers which leaves a particularly large
basal area free (see Plate III, Figure 1). A typical protective membrane
connects the third with the fourth pair of arms.

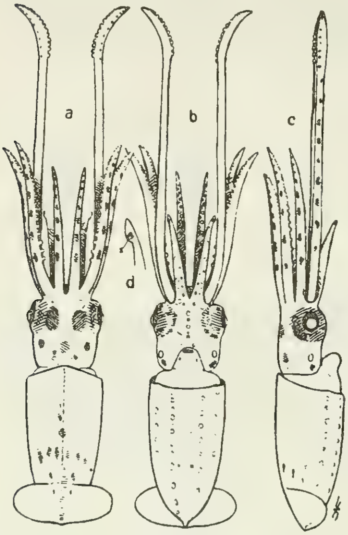

FIGURE 141. Young form of Abraliopsis morrisi. from the Naples plankton collected in May 1912, slightly reconstructed after the specimen shown in Figure 2 of Plate IV. 5×. Note the general proportions, especially of the arms; the marked modification of the gladius; the arrangement of chromatophores (some of them are bleached) in comparison with Figure 140; the pattern of luminous tubercles on mantle, head, ventral arms and eyes; the knoblike swellings on the apex of the ventral arms with the dark luminous organ. (The small drawing shows the apex of the right ventral arm at higher magnification. The dot (x) on the dark organ is a chromatophore).

The tentacles are very long, almost as long as the body behind them. The club occupies about one quarter of the tentacle. The club bears proximally 2 rows of suckers, and the growing distal part 4 such rows, including a median row in which 2 suckers begin conversion into hooks and are much larger than the others. The tentacles still form part of the arm circle at the base. They appear as a fourth pair of arms, in which case the ventral arms would have to be designated as the fifth pair (cf. p. 115). Buccal funnel and mouth cone resemble those of the following stage.

Of particular interest are the "anlagen" of the luminous organs. They are arranged symmetrically in 4 pairs on the mantle, one on the funnel, one pair on the eyelid behind the lens, one on the eyelid in a ventral median direction from the lens, and 4 in a curve on the eyeball (Plate IV, Figure 2). The latter organs appear as flat, dull, whitish spots. On the other hand, the superficial organs form small, very low tubercles. The arrangement of the chromatophores is almost exactly as in the preceding stage, i. e. each chromatophore has its homologue.*

292 The conspicuous knobby swellings at the apex of the ventral arms are "anlagen" of luminous organs. The presence of these structures proves that these specimens belong to Abraliopsis. Comparable stages of Abralia have instead normal ends of arms. These swellings are probably modified superficial organs.

The next stage (Figure 141) markedly resembles the adult but still resembles the former stage in habitus. The surrounding of the gladius is already complete; only the keel of the rhachis and a small part of the flag are still visible through the dorsal skin. In the mantle sac the gladius has already attained the form characteristic for young Enoploteuthinae (Figure 106b). The fleshy apex behind the cone has become more distinct, but is still rather small (see also Plate IV, Figure 2).

The fins begin to have their definitive form. They are much longer at the base and also markedly produced laterally. Mantle margin and funnel apparatus resemble those of the preceding stage. Noteworthy on the head is the normal displacement of the eyes, which at first become larger and laterally projecting, and then turn gradually laterally, occupying the sides of the head instead of the anterior corners.

The arms have become still longer. The third pair is now longer than the second pair. The tentacles are essentially as in the preceding stage. The suckers are biserial at the base, then form 2 zigzag rows and 4 rows distally. Two suckers of the ventral inner row of the hand part of the club are enlarged and show indications of conversion into hooks: their opening is proximal, and the distal part is produced into a hood (see Figure 52f on p. 131). A similar tendency to modification is distinct in the arm suckers; their distal side is projecting, as if swollen, but the margins are still rounded.

All arms bear protective margins, which were already indicated in the former stage, particularly the protective margins on the ventral inner edge of the second and third pairs. These are continuous margins, the supports of which project distinctly and push the margin out. The number of supports is the same as that of suckers on the entire arm at least in the more distinct ventral margins. The supports are thus coordinated not only to the suckers of the ventral row but also to those of the dorsal row. This primary condition of Decapoda (p. 116) resembles that in the Cirroteuthidae (cf. Chapter 48) if the cirri are considered as homologous to the supports, as we have done. The supports have the distinct character of cirri, i. e. they are independently mobile processes, while the connecting margin is accessory (a similar condition is present in Architeuthis). In Abraliopsis this condition is connected with the arrangement of the suckers: they form proximally a loose biserial pattern or rather a zigzag row which is often nearly a single row; they are thus almost equally related to both protective margins, a condition which may be a reversion to a primitive state.

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* Issel (1920) established the constant pattern of the larval chromatophores in the species and the general regularity of their distribution in the Oegopsida. I can only confirm his results. Further details will be given in Vol. III.

293 The buccal funnel (Plate III, Figure 1) shows the characteristics of all young Enoploteuthidae. Around the mouth cone are the inner and outer lips, surrounded by 8 distinct supports ending in 8 points. The supports are associated with the edges of the basal arm parts as follows: both dorsal pairs with the median edges of the arms; the third pair less distinctly with the ventral edges of the third pair of arms; the fourth pair with the dorsal (lateral) edges of the ventral arms. Weak skin folds (attachments) are present on these edges. The connecting membrane between them reaches the bases of the arms slightly lower down, so that buccal pockets are formed on each side between the first and second, second and third, third and fourth support. No pocket is formed between the dorsal and ventral supports of each side, but the dorsal protective margins of both upper arm pairs and those of the ventral pair later become connected with the bonds, as in Pyroteuthis and Abralia. The ventral protective margin of the third pair ends slightly ventral to the bond as in these two genera.

The formation of luminous organs has considerably advanced. On the mantle the luminous organs form now 4 longitudinal rows, each with a large number of luminous tubercles in a different stage of development. The median rows include the longitudinal row of 3 organs already present in the former stage which can still be easily identified but their position is less regular. The lateral rows resemble the lateral organs of the preceding stage, but contain fewer tubercles than the median rows. A pair of new "anlagen" has developed on the funnel between the previously present organs, forming a transverse row with them. On the head, the "anlagen" of the later larger superficial tubercles are now present. Two of them are situated before the funnel and another three form a median longitudinal row; one at the base of the tentacles and the ventral arms, on which there is also a longitudinal row of 5 organs (if they are distinct). Other luminous organs are the knobby swellings at the apex of the ventral arms and the 4 organs on the eyeball (the 5th is still absent, p. 288). There are also 2 small superficial organs on the eyelid, as in the preceding stage, one near the posterior margin, the other nearer the upper margin. Each arm of the second pair bears dorsally a distinct basal organ.

An opened mantle cavity of this stage is shown in Plate IV, Figure 2. This figure is of more general than special interest. Similar stages of other Enoploteuthinae show almost the same characters as the young forms of all typical Metateuthoidea (cf. Figure 88; Vol. II, Plate VII, Figure 4). The following characters are specific for the Enoploteuthidae: 1. The form of the funnel bonds, which still closely resembles the general form in the Oegopsida. 2. The trifurcation of the posterior aorta. The strictly oegopsid character of this stage is recognizable from the fact that the vena cava bifurcates behind the hind intestine and funnel sac, and not before them, as is typical for other Cephalopoda (p. 231, Figure 109a). Other superficial or deep-seated organs show the typical characters of the Teuthoidea, Decapoda or even Dibranchiata. The gills, branchial spleen, gill ligament, branchial hearts, abdominal veins, posterior aorta, venous appendages, hind
294 intestine, ink sac, the vena cava (before the anus), anal papilla, stomach and a caecum are typical in form and position.

A young specimen from Messina (Figure 142) shows an important transition to the definitive stage. The relationships between gladius and mantle are mainly unchanged, but the fins cover a greater part of the end of the gladius. Comparison with Figure 137b shows that the fins have reached their definitive form: their length is about half of the mantle length. Because of preservation in formol, the fins appear narrower, perhaps because of shrinkage, and with a rounded, heart-shaped outline. The "ear-lobes" are already indicated.

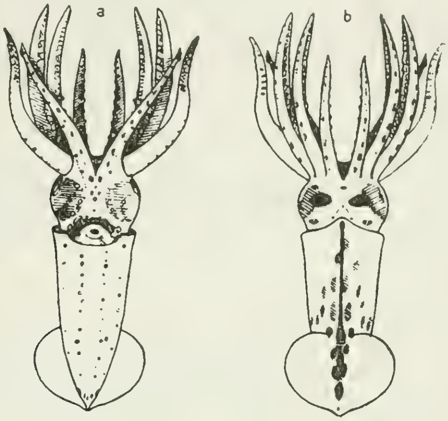

FIGURE 142. Young Abraliopsis morrisi from Messina (July 1911). 5×. The following characters are more distinct than in the preceding stage: modification of the fins (which are slightly wider in life); enlargement and displacement of the eyes; the growth of the ventral arms; modification of the clubs; formation of hooks and protective margins on the arms and the relative shortening of the arms.

The olfactory papillae are situated lateral to the funnel; the low, wide elevations medially and anterior to the papillae belong to the boundary of the funnel pit, the lateral end corresponds to the ventral (fourth) longitudinal fold of the neck (see Figure 137). The eyes are very large and displaced laterally, resembling the definitive form of the head. Arms and tentacles are relatively shorter than in the preceding stage, perhaps due to preservation. The tentacles are particularly thick; they taper toward the clubs, which are whiplike at the end (Figure 127).

The length of the arms is different at this stage. The third pair is now as long as the second; the fourth is only slightly shorter than the second and much longer than the first. The suckers of the arms are converted into hooks which still resemble the form of suckers except on the basal and distal part (hooklike suckers). The protective margins show the characters described above (p. 293). They are wide on the ventral sides of the second and third pairs of arms, but weak or rudimentary elsewhere. There are hardly any indications of protective margins on the clubs. The basal suckers of the club are still distinctly biserial. The carpal group consists of 4 large suckers on each side. There are 6 suckers on the left side and 5 small ones on the right side before the hand part, some of which fall off later. There is a ventral median row of 3 larger hooks on each side of the hand part; the adjacent marginal row has already been lost. The dorsal median and
295 marginal rows still contain small round suckers, the short distal part 4 rows of small suckers which decrease in size ventrally.

The arrangement of luminous organs is more or less as in the preceding stages, but their number is larger. There are still only 4 organs on the eyeball; one organ is apparently absent behind the large anterior organ. The terminal swellings of the ventral arms are more complicated. There is another organ distal to the first, and the apex probably grows further. The arrangement of the chromatophores closely resembles that of the preceding stage, but their number is larger; many chromatophores are bleached.

296

Chapter 16

GENUS THELIDIOTEUTHIS
Pfeffer, 1900

Only one species

THELIDIOTEUTHIS ALESSANDRINII
(Vérany, 1851) Chun, 1910

DIAGNOSIS

Apex of posterior end weakly developed, curved ventrally in preserved specimens. Fins large, rounded, occupying about four fifths of the mantle length; fin span wider than length of mantle. Mantle broad, sac-shaped. Neck folds distinct. Ventral arms shorter than the lateral pairs. Arms with hooks, except at the end. Tentacle clubs with 4–6 carpal suckers; hand part with a dorsal median row of 7–9 larger hooks, a ventral row of 7 smaller hooks, suckers of dorsal marginal row lost. Luminous organs on eyeball absent. Head and mantle with only a few (18) larger luminous tubercles. Luminous organs also present on tentacle stalk (one ventral on the base, 6–12 on the outer side).

LITERATURE

1851 Vérany, Loligo alessandrinii (p. 99, Plate 35, Figs. f–h).
1857 Troschel, Enoploteuthis polyonyx (p. 67, Plate 4, Fig. 9).
1880 Steenstrup, Loligo alessandrinii (p. 96, Note 3).
1880 Steenstrup, Onychia caribaea (ibid.).
1882 Verrill, Abralia megalops (p. 364).
1884 Verrill (Suppl. Rep.), Abralia megalops (p. 105, Plate 3, Fig. 4).
1884 Verrill (: Trans. Conn.), Abralia megalops (p. 143, Plate 28, Fig. 2; Plate 34, Fig. 2).
1884 Pfeffer, Enoploteuthis pallida (p. 18, Figs. 23, 23a, 23b).
1889 Carus, Loligo alessandrinii (p. 449).
1889 Carus, Abralia polyonyx (p. 449).
1889 Appellöf, Calliteuthis alessandrinii (p. 27, Figs. 7–11).
1900 Pfeffer, Thelidioteuthis polyonyx (p. 167).
1910 Chun, Thelidioteuthis alessandrinii (p. 104, Plate VII, Figs. 16/17).
1912 Pfeffer, Thelidioteuthis alessandrinii (p. 178, Plate 18, Figs. 1–29).
1916 Naef (synopsis), Thelidioteuthis alessandrinii (p. 16).
1921 Naef (Syst.), Thelidioteuthis alessandrinii (p. 537).

An adult Thelidioteuthis has not been found in Naples, but I have a young larva which has not been described before and which undoubtedly belongs to this genus. I shall give a brief description of the adult after Pfeffer (1912, Plate 18) to prove this.

297 STRUCTURE OF THE ADULT ANIMAL

Thelidioteuthis differs from other Enoploteuthidae in the short and thick body, the blunt posterior end, the markedly rounded fins and the particularly long arms.

The gladius has a short free rhachis, a very wide flag with rounded outline and a flat, spoonlike cone which is surrounded by the muscular mantle except for the keel of the rhachis. The fins are very large, about four fifths of the mantle length. Their span is markedly wider than the mantle length. The fins differ from the typical form shown in Figure 137 in the marked rounding of the lateral corners and the anterior and posterior margin so that they form more a transverse oval than a rhombus. The slender apex of the posterior end of the body is curved ventrally in the preserved specimens and may be overlooked (cf. Octopodoteuthis). The posterior end is probably slightly pointed in the live animal. The mantle sac is otherwise stout, sac-shaped, nearly twice as long as wide, with a rounded end.

The longitudinal and transverse neck folds are typical, but the fourth longitudinal fold is only indicated in the corner where the anterior transverse folds pass into the indistinct marginal edge of the funnel pit.

The eyelids, buccal funnel and funnel apparatus are typical. The funnel bond is relatively wide and short but otherwise resembles that of other Enoploteuthidae; the corresponding mantle bond is unusually short, shorter than the funnel bond.

The arm formula is 3, 2; 4, 1, i. e. the lateral pairs are much longer than the others; the third pair is only slightly longer than the second, and the 4th slightly longer than the first. At any rate, the fourth pair is never longer than or as long as the lateral arms, as in other Enoploteuthidae. Each arm bears 18–24 hooks which occupy its greater part and are more numerous on the lower arm pairs than on the two upper pairs. Several pairs of larger suckers are situated distal to the hooks, followed by several pairs of smaller suckers which become very small toward the apex. The hooks of the fourth pair of arms are also smaller than on the other arms. Slightly widened swimming margins are present on the three upper pairs; they are best developed on the distal part of the third arm. All arms have typical protective margins.

The tentacles have a dorsoventrally compressed stalk with a narrow inner surface which is bordered by edges and has a median longitudinal groove. The club is not or only slightly widened, Its carpal part bears 4–6 suckers and a few more knobs and is indistinctly separated from the hand part. The carpal pad is bordered anteriorly and laterally, as in the Onychoteuthidae. The ventral median row is replaced by 8–9 large hooks, and 7–8 smaller (rotating) hooks are situated on the position of the dorsal row; the ventral marginal row is partly retained, but the dorsal marginal row is lost. The distal part contains

298 a few oblique rows of four hooks. Except for the carpal suckers, the suckers bear sparse teeth, at least on the distal margin. Protective margins are present on each side of the club but are better developed on the dorsal than on the ventral side.

The superficial luminous organs form large, markedly projecting tubercles. They are much less numerous than in the Enoploteuthinae. They have the same distribution on head and mantle as in the young stages of Abraliopsis (or in the Enoploteuthinae in general). On each side of the mantle (i. e. ventrally and laterally) there are 11 organs in 3 longitudinal rows which alternate, forming straight and oblique transverse rows.

The ventral side of the head bears a superficial luminous organ on the eye and obliquely anteriorly and median to the olfactory tubercle. A further organ which appears to be situated on the head but is actually located ventrally on the base of the tentacle stalk, is visible through the membrane between the third and fourth arm (as in the young Abraliopsis, Figure 141b). There are apparently no luminous organs on the eyeball. Five such organs, however, are situated on the lid margin on the side of the head. Three of these organs are dorsal, one behind and one below the opening of the lid. The latter two organs correspond to those of the young Abraliopsis (Figure 141). There are also superficial luminous tubercles on the outer side of the tentacle stalk — about 12, forming pairs and alternately larger and smaller. (In the young Mediterranean animal (Figure 144 on p. 300) there are only 6, corresponding to the larger organs.)

The consistency of the body is more gelatinous than in the Abralia-like forms. The dark chromatophores are reddish brown, the light ones brownish yellow.

YOUNG FORMS

The young stage described below certainly belongs to this species. It was collected in the Naples plankton on 19 January 1903. At first glance it resembles a young Abraliopsis (Figure 140). I considered it at first as a small Abralia, i. e. the most closely related form, because it differs markedly from Abraliopsis. Above all, the consistency of the flesh is different, it is markedly transparent and gelatinous even after preservation. The flesh of the live animal is therefore certainly extremely delicate and transparent. The animal is also much larger than the comparable stage of Abraliopsis.

The form of the head differs from that of the same stage of Abraliopsis: the eyes are already beginning to be displaced laterally (cf. Figures 141 and 142). Particularly interesting is the anterior part of the head ("forehead"), a distinct area situated between the eyes and arms and supported by the muscular arm pillars. The forehead is transparent laterally also in the preserved animal so that the arm support, typically situated between the eyes, is clearly visible as a light body. This emphasizes only the general type of connection between head and arms in the Decapoda, especially in the Teuthoidea. It explains the formation of the characteristic structures in the Chiroteuthidae (Figure 190) and especially in the Cranchiidae (Figure 199), 299 and also the appearance or persistence of stalked eyes (cf. Vol. II, Plate IV). One has only to assume an invagination of the skin into the transparent gelatinous part of the forehead, causing the disappearance of this unnecessary tissue. The arm circle and eyes are already normally independent of each other.

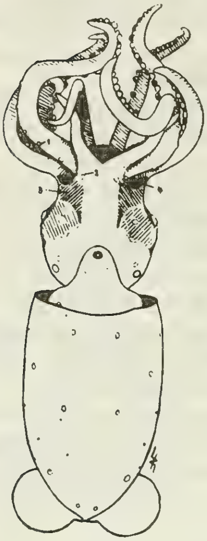

FIGURE 143. Young stage of Thelidioteuthis alessandrinii. 5×. Collected on 19 January 1903 in the Naples plankton. Note the resemblance with Figure 141 and the distribution of the luminous organs connected with certain chromatophores on head, mantle and tentacles, the form of the forehead (at 3) and the head as a whole.

1 — Luminous organ of the tentacle stalk; 2 — same, visible through the protective membrane at the base; 3 — gelatinous mass of "forehead"; 4 — indication of the tentacle pockets. (Cf. also Figure 88.)

The general appearance is that of a typical larva of Enoploteuthidae. The relationships between mantle and shell are as in Figure 140, i. e. not only the rhachis but also a large part of the flag (lanceola) is free of the muscular mantle. The fins are connected only at the posterior end by a straight, transverse edge. The fins are rounded, nearly circular. The 3 corners of the mantle margin are only indicated. The funnel apparatus resembles that of the young Abraliopsis. The eyes have begun their lateral displacement; the olfactory organs still retain their typical early larval form and position but are beginning to be displaced toward their position in the adult. A sinus is already recognizable on the lid margin.

Particularly interesting is the arm apparatus. The second pair is still the longest; the third pair is already as long as the first but still much shorter than the second, while the fourth pair is only about half as long as the third (Formula: 2, 1 = 3, 4). Apical swellings on the ventral arms are absent. All arms bear 2 rows of suckers which are much smaller on the ventral arms. Rudimentary protective margins are already present at least on the ventral side of both lateral arm pairs, closely resembling those of Abraliopsis. The number of supports and points equals that of the suckers in the dorsal row, i. e. the number of supports and points equals the number of suckers on the arm. The condition in Abraliopsis and Architeuthis (cf. p. 287) becomes thus more important morphologically.

300 The tentacles are distinctly flattened dorsoventrally. About a quarter of their length is occupied by the club (Figure 144), which shows the characteristics of the youngest stage of Thelidioteuthis. A small, slightly isolated sucker is situated at the base of the club. Then follow 1 or 2 medium-sized suckers, and then 3 pairs of larger suckers, representing the future carpal part. Further distally are 3 alternating pairs so that there are 4 rows in which the outer sucker is always larger than the inner. There are 4 distal rows of suckers which decrease rapidly in size and later form the hand part. The hand part thus develops a pattern in which the marginal rows contain at first much larger and more differentiated suckers than the median rows, which probably become functional only after the conversion of the suckers into hooks and replace the function of the marginal rows. (This is a modified form of the typical division of labor, p. 127.)

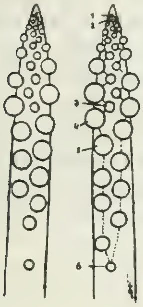

FIGURE 144. Tentacle clubs of larva of Thelidioteuthis, showing the arrangement and size of the suckers. Note the small suckers in the median rows of the hand part which are later converted into hooks and which meanwhile remain "anlagen."

1 — Recently formed "anlage" of sucker; 2 — anlage of sucker of the distal part; 3 — future hooklike sucker of the hand part; 4 — dorsal marginal sucker of the hand part (which becomes reduced and falls off); 5 — carpal sucker; 6 — small sucker of the reduced stalk part.

Particularly important is the distribution of luminous tubercles in the larva. Comparison with the drawing of Pfeffer (1912, Plate 18, Figure 1) shows that the existing tubercles are typical in position although many are still absent. The mantle bears 6 of the 11 later organs on each side; the third tubercle is absent in the median rows (counting from the anterior end), the middle tubercle in the following rows and the 3 posterior organs in the lateral rows. The 4 organs on the ventral side of the head are present, but the 5 organs surrounding the lid opening are still absent. There are 7 organs on each side of the tentacle stalk, the first of which is situated at the extreme base. It is covered, completely on the left, partly on the right, by the protective membrane between the third and fourth pairs of arms. This organ does not form a particular type as it is situated exactly in line with the others. If it is later completely ventral, as reported by Pfeffer (1912), this must be due to displacement.

301 *Chapter 17*

FAMILY ONYCHOTEUTHIDAE
Gray, 1849

DIAGNOSIS

Habitus typical. Rostrum consisting of conchioline, attached dorsally on the cone, directed obliquely posteriorly and upward, and supporting the apex of the body. Ventral buccal pillars attached to median side of ventral arms. Neck folds completely developed, sometimes additional folds present. Arms with 2 rows of suckers. Hand part of tentacle club: suckers of ventral median rows usually developing into large, fixed prehensile hooks; dorsal rows forming small rotating adhesive hooks. Suckers and knobs of carpal part forming a rounded, distinctly delimited "adhesion pad." Tentacle stalk without suckers. Sexual dimorphism in the arm apparatus not observed.*

TYPICAL STRUCTURE OF THE ADULT ANIMAL

The Onychoteuthidae are without doubt closely related to the ancestral form of the Oegopsida and our concepts on the primary constitution of the family are therefore important for understanding the other groups.

The habitus of Onychoteuthis, the best known genus of the family, may be considered as typical (Figure 153) and also the topographical relationship between mantle and shell. The gladius is visible through the dorsal skin as a dark median line. The keel of the rhachis is not surrounded by the muscular mantle (Figure 66 on p. 157). The keel bears a "crest,"** a narrow dorsal longitudinal ridge, especially in the posterior part, to which the rostrum is attached posteriorly. If this crest is present, it alone reaches the skin (i. e. the surface). The rest of the rhachis is covered by the
302 muscular mantle, which extends to the ridge. The rhachis has a blunt, parabolic anterior end; the flag is connected to the posterior two thirds of the rhachis so that the form of the gladius resembles that of Loligo (Figure 63 on p. 150). The flag is connected posteriorly with the distinct

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* Tetronychoteuthis Pfeffer differs from all other genera of the family in the structure of the tentacle club. This genus shows some juvenile characters, in that its club bears neither hooks nor carpal pad, but it still has some stalked suckers proximally. It is a distinctly larval (neotenic) type.

** The ridge if formed by the periostracum, because all 3 layers of the shell of Dibranchiata have to be assumed to be present in the gladius (cf. p. 52).

but shallow cone which bears dorsally a large rostrum, which is characteristic for the family and typical for the Teuthoidea (cf. Figure 72 on p. 171). The rostrum forms a laterally compressed spine which does not continue in the cone axis but is curved posteriorly and upward. The rostrum does not occupy the whole outer side of the cone but only a dorsal part which begins at the apex of the cone, extends to the outer side of the rhachis and ends in the ridge. The rostrum supports the posterior apex (which is fleshy in other Oegopsida). The fins are attached dorsally to the apex, and the posterior end is raised from the posterior end of the mantle sac. This condition causes the fins to be placed in the direction of swimming (cf. Pfeffer, 1912, Plate 3, Figure 20). This is obviously not a primary condition (Figure 32 on p. 107). The ventral curvature of the dorsal line caused by the spindle-shaped form of the mantle sac which is otherwise useful (Figure 53 on p. 136) causes the oblique position of the fins of Teuthoidea also in the adults.

The fins are large, of typical form, i. e. transverse rhomboidal to heart-shaped, with rounded anterior margin, distinct "earlobes," a slightly angular posterior end and a blunt lateral corner. The base of the fins occupies at least two fifths of the mantle length.

The neck folds are almost typical, including 2 transverse and 4 longitudinal folds. However, there are some special characters. The fourth (ventral) longitudinal fold does not reach the posterior transverse fold but ends free (Figure 153b). The olfactory tubercle is situated at the posterior end of the third longitudinal fold, it is pushed toward the free margin of the fold and even forms a projection of the fold (cf. p. 286). As in the Enoploteuthidae, this is apparently preparatory for a free, stalked olfactory tubercle. The funnel pit is moderately deep, with a marginal edge. If the funnel is curved back as shown in Figure 153b, the inner and outer funnel adductors become visible.

The eyelid is typical, with a distinct sinus at the anterior margin in the adult. There is at least one window on the ventral side of the head under the middle of the eyeball.

Swimming margins are present on the 3 upper pairs of arms. Those of the dorsal arms are present only in the distal half of the arm and are very weak, but typically mediodorsal (Figure 79 on p. 180). On the two following pairs, the margins are large, especially on the third pair, and occupy the whole length of the arm. The swimming margin of the second arm is connected with the ventral outer edge at the base. On the third arm, the margin ends on the outside between the two edges but nearer the ventral edge. It is widest slightly before the middle of the arm, where it forms a corner, tapers proximal and distal to this point, forms a low edge at the base and then rises abruptly.

303 These characters are perhaps typical for all Metateuthoidea and could be considered as a further development of the conditions described on p. 136. The ventral arms have normal outer margins. The protective margins are weak, with only indicated supports the number and position of which corresponds to those of the suckers in the adjacent rows. The suckers are cup-shaped, biserial, without distinct dentition (Plate XII, Figure 3; cf. p. 130). A kind of wart is usually present on their soft distal outer margin.

The tentacles are long and sharply separated into stalk and club. At the base of the club is a raised oval pad which is surrounded by a fine edge and bears about 10 suckers and knobs. These still show the primary arrangement in oblique rows of four (Figure 52 on p. 131). The hand part occupies most of the club. It bears 2 marginal rows of small, rudimentary, perhaps deciduous suckers and 2 median rows of hooks. All, except the proximal and distal hooks of the ventral row (about 6–8), are of the prehensile type, large, long and particularly strongly attached (p. 131). The others are "clasping hooks," i. e. much smaller, with thin stalks which can rotate in a slightly sunken, concave articulation pit. The distal part bears only small suckers, in a few rows of four.

The distal two thirds of the club have strong swimming margins. The protective margins are incompletely developed, the dorsal margin being distinct only on the proximal half of the club and the ventral forming an edge in the distal part and widening like a lobe in the proximal third of the hand part (cf. Figure 138 with Figure 154), as in the Enoploteuthinae.

The buccal funnel shows the typical characters (Pfeffer, 1912, Plate 1, Figure 1; Plate 7, Figure 2; Plate 9, Figure 8; Plate 12, Figure 7; Plate 14, Figure 13), but both ventral supports are attached to the median edges of the ventral arms, so that they differ from those of most other Oegopsida, especially from the related Enoploteuthidae, e. g. Lycoteuthis (Figure 126; compare also the Chiroteuthidae and Cranchiidae).

The funnel part (Figure 155) is characteristic for the Oegopsida and even for the Teuthoidea in general (cf. Figure 57 on p. 140) and the same applies to the situs of the mantle cavity. Except for the luminous organs, the situs of the mantle cavity may be considered as a starting point for the morphological interpretation of this part of the body in the Oegopsida (Figures 155, 157). Luminous organs are present in a very characteristic form in the mantle cavity also in some Onychoteuthidae (Plate IV, Figure 1). Thus, an anterior luminous organ is situated below the hind intestine and near the anus of Onychoteuthis, Chaunoteuthis and Cycloteuthis (p. 312) and probably corresponds to the left anal organs of the Lycoteuthinae and Enoploteuthinae, but it may also have been formed by the fusion of a paired organ. Characteristic is the posterior organ, which is certainly homologous to the left organ in a similar position on the ink sac of Octopodoteuthis and Chiroteuthis, but not homologous to the interbrachial organ in Figure 128 (cf. Plate IV, Figure 3). There were, therefore, at first 2 pairs instead of the two single organs of Onychoteuthis in the ancestral form of the Onychoteuthidae and it probably also had further organs which have been lost; the condition in Onychoteuthis is typical
304 for the family. The Onychoteuthidae also have other, until now overlooked luminous organs on the ventral side of the eyeball which are directed slightly inward and anteriorly. In Onychoteuthis and Chaunoteuthis I found at this point a number of large, oval, yellowish brown elevations which probably represent the whole complex of organs present in the Enoploteuthidae and correspond to those of Chiroteuthis (Plate IV, Figure 3) and Ctenopteryx (Plate III, Figure 4).

The jaws of Onychoteuthidae are typical for the Teuthoidea, with the special character of the Oegopsida discussed on p. 229 (Plate XVII, Figures 4, 5). The same applies to the radula (Plate XV, Figures 2, 3).

Hectocotylization has not been observed. This has to be considered typical and not accidental, because numerous adult specimens of both sexes of several genera have been obtained. This is not surprising as the Oegopsida do not show a general type of hectocotylization (p. 232).

In the mantle cavity the form of sexual dimorphism which is typical for the Metateuthoidea shows some slight variations (Figure 155). The distal part of the male duct projects as a very thin, long, free genital process from the genital pocket and the pocket of the gill base (the genital pocket opens inside the latter). Female genital processes are absent, at least in the half mature specimens I have examined. The female egnital opening is situated inside the pocket of the gill base (cf. p. 213); the oviduct glands or their proximal part is visible near the branchial hearts, behind the branchial root. The nidamental glands are situated in the typical position.

POSTEMBRYONIC DEVELOPMENT OF THE ONYCHOTEUTHIDAE

The youngest planktonic stages are typical larvae of Oegopsida which show some characters of the family and can therefore be distinguished without difficulty from specimens of similar size of Enoploteuthidae, their closest relatives. However, the species cannot be determined with certainty and I describe therefore here my youngest specimens. Compare also Chun (1910, Plate VII, Figure 12), where a larva of Onychoteuthidae is illustrated as "Abraliopsis."

(305)

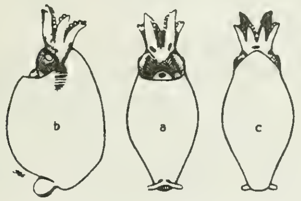

FIGURE 145. The youngest larva of Onychoteuthidae from the Naples plankton (probably Onychoteuthis banksi). 10×. The specimen is strongly deformed by preservation; the gladius is curved so that the fins are now ventral.

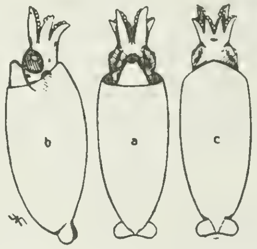

FIGURE 146. The same stage as in Figure 145, but reconstructed by observation of live specimens. The fins already resemble those of the later stages. The other characters are those of a typical, very young larva of Oegopsida. Note the formation of the arms, in which the third and fourth pair are very small tubercles.

The earliest postembryonic stage which I have in a well preserved specimen is shown in Figure 145. It is slightly deformed by contraction during preservation. Figure 146 is a reconstruction based on observation of live animals. The arms and fins are also contracted by preservation (cf. Figure 131).

I could not distinguish the gladius, but it probably resembles that shown in Figure 140. The fins are connected at the posterior end but diverge markedly at the base. They do not yet show the distinctly differentiated outline of young Enoploteuthinae (Figure 143).

305 Funnel and head show the typical characters of the early larvae, which are still more distinct in the following stage (Figure 147). As in the youngest stages of other Oegopsida, the mantle cavity contains only "anlagen" of featherlike gills (Figure 111). The arm apparatus is more or less characteristic. It consists of 6 nearly equal arms, each with 2 short rows of suckers. These arms correspond to the first and second pair and the tentacles; the third and fourth pair are still in the form of small papillae.

Figure 147 shows a slightly later stage of the typical development of the Onychoteuthidae. This larva closely resembles a larva of young Loliginidae (Figure 88), although the arm apparatus shows the typical characters of the Oegopsida and the posterior end already shows the specific characters of young Onychoteuthidae.

The gladius is apparently already rather slender, as is characteristic for the Onychoteuthinae, but already surrounded by the muscular mantle in its greater part. Only the rhachis and a narrow median stripe of the flag are still visible through the dorsal skin. The short conical cone and the small, still terminal rostrum are visible posteriorly. The muscular mantle is attached at the margin of the cone. The fins are rounded. They have already advanced slightly anteriorly but do not yet reach the apex, which therefore projects freely, and consists only of a rostrum covered by the shell sac and skin ("shell fold"). The sharp rostrum has perforated the skin in this and other similar specimens. This is due to impact of the larvae against the net and vessels during capture and partly to contraction of the mantle during preservation, a process opposed by the gladius. This obviously is not normal (cf. Sepia orbignyana).

The funnel apparatus shows the typical characters of such stages. The neck bond is distinctly delimited, slightly widened anteriorly, in the form of a narrow platelet with 2 lateral longitudinal grooves. Funnel bonds are still
306 absent or indistinctly delimited. The head has the typical juvenile form of the Teuthoidea, especially with regard to the relationship between eyes and the other parts. The olfactory papillae are situated far in front of their normal position. The lid margin is still round and its width and position are very variable in these stages.

The tentacles are now longer than the other arms and have a different arrangement of the suckers. The suckers at the end of the tentacles are already quadriserial, while the arrangement is still biserial in its greater part. The small stumps of the third and fourth pair of arms on each side are connected by a low protective membrane which separates the base of the tentacles from the complex of arms to which the tentacles belong according to position and development. The "anlagen" of the buccal funnel appear in this stage.

The situs of the mantle cavity more or less resembles that of the later stage described below (Figure 149).

The stage shown in Figure 148 differs mainly in size and preservation from the larva described above. This stage is 0.25 times larger but lags behind in the development of some parts. I therefore assume that the two larvae belong to Ancistroteuthis and Onychoteuthis, but I cannot decide to which genus, not even with the help of older specimens.

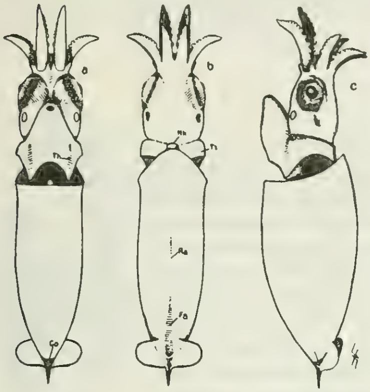

FIGURE 147. A young larva of Onychoteuthidae (Ancistroteuthis or Onychoteuthis) from the deep plankton of Naples. 10×. Slightly reconstructed. The anterior part of the body of the live animal does not project so strongly from the mantle sac; it is shown here as in the specimen to show the parts of the funnel apparatus and mantle cavity. The anterior part of the body is retracted into the mantle. Note the development of the arms, which have slightly progressed. The head shows the typical characters of very young Teuthoidea (cf. Figure 88). Also the funnel apparatus, which has an oblong rectangular neck bond but still no funnel bonds. Most characteristic are the form of the posterior end and the attachment of the fins.

The typical habitus of such larvae is shown better in Figure 148 than in Figure 147, except for the posterior end, which is also deformed, although it can be reconstructed after Figure 149. The ventral part of the mantle is retracted from the attachment at the margin of the cone, and the posterior end of the gladius is strongly curved ventrally. It is almost impossible to avoid such a deformation during preservation (cf. concluding Section 3).

The posterior end resembles otherwise that of the preceding stage. The fins are slightly larger. The typical corners are distinct at the anterior
307 margin of the mantle. The funnel is large, projecting and slightly sac-shaped. In the live animal, the funnel is even longer and its opening projects to before the head (cf. Figure 111). The arms resemble those of the preceding stage (Figure 147), but the apex of the tentacle shows hardly a transition to a quadriserial arrangement and the connection between the third and fourth arms is still not recognizable.

Figure 149 probably represents the same species, Onychoteuthis banksi after opening of the mantle cavity. This specimen is markedly larger and slightly further developed. The third pair of arms is longer than the fourth and already bears 2 rows of small suckers. The connection between the third and fourth arms is not yet completely developed but has begun on the fourth arm. The apex of the tentacle, however, bears suckers in a distinct quadriserial pattern.

The funnel apparatus is typical, with bonds of characteristic form. The funnel retractors are wide, bandlike, projecting like a septum into the mantle cavity. The gills are nearly comparable in development to those of a freshly hatched larva of Loliginidae (Figure 88). The gill ligaments, efferent branchial vessels, branchial hearts, venous appendages, renal papillae, vena cava, hind intestine and ink sac closely resemble those of a newly hatched Loligo vulgaris, i.e. they are typical for young Teuthoidea (cf. also Abraliopsis, Plate IV, Figure 2). On the other hand, the area behind the gills is much longer, as are the superficial vessels in this area (posterior aorta and posterior pallial veins). The posterior aorta branches in the form typical for the Oegopsida. The median pallial septum is restricted to the posterior part of the mantle cavity and the median pallial artery begins accordingly also far posteriorly, but there is still a common trunk of the two posterior pallial arteries, which supply the fins (in contrast to the Enoploteuthidae, p. 264).

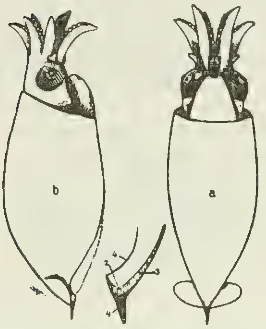

FIGURE 148. Young stage of Onychoteuthis (or Ancistroteuthis) from the deep plankton of Naples. 8×. The posterior end is deformed but can be reconstructed after Figure 149 as follows: the posterior part of the gladius should be more extended and the ventral median line of the mantle should pass in the continuation of the cone (dotted in b). The spine would then be directed obliquely upward and posteriorly. The general habitus resembles that of the live animal, in contrast to the preceding figure. Head and arms resemble those in Figure 147. The funnel is very large and extended but smaller than in the live animal. The small central drawing is an optical median section through the posterior end of the gladius of a younger larva. The rostrum is still attached terminally on the apex of the cone.

The fins of this stage extend almost to the apex of the rostrum which is situated between them as a transition toward the next stage.

308 The stage shown in Figure 150 is further developed. The gladius is more completely surrounded; the keel of the rhachis is visible at some points through the skin. Also visible is the lanceola, a narrow area between the fins, which tapers rapidly anteriorly and more gradually posteriorly. The fins have a posterior point which passes in a curve toward the rounded lateral margin. The fins have grown markedly anteriorly and occupy one fifth of the length of the mantle.

The eyes are much larger and laterally displaced so that their rounded definitive form is gradually prepared. The fourth pair of arms begins to grow and already bears 2 short rows of partly developed suckers. The third pair has also become larger and is already connected with the fourth pair.

Figure 151 shows a very similar following stage. The general form of the body resembles that of an adult, but the arms are still small and partly larval in form.

All that is visible of the gladius is a wedgelike figure between the fins, rapidly tapering anteriorly to a narrow stripe corresponding to the keel of the rhachis and occupying the whole midline of the body. Cone and rostrum are visible ventrally, forming a narrow apex. The fins project in a point posteriorly; they are rounded laterally, without corners or "ear-lobes." The mantle is thick, spindle-shaped, with the 3 normal anterior corners.

The eyes are still further enlarged and the olfactory papillae are situated nearly in their definitive position. The eyelid is still rounded, the funnel as large as in the larva. Marked progress is evident in the arm apparatus. The ventral arms have grown further; the lateroventral arms are longer than two thirds of the second pair, which was already much longer than the first in the preceding stage. The formula at this stage is 2, 1, 3, 4. A swimming margin appears on the distal part of the second pair but this is not visible on the third and first pair. The tentacles are very delicate. The club bears 2 basal and 4 distal rows of suckers. The buccal funnel is weak but distinctly developed, consisting of 7 parts.

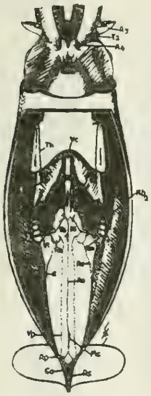

FIGURE 149. Young stage of Onychoteuthis banksi or Ancistroteuthis lichtensteini, after removal of the ventral part of the muscular mantle. 8×. Note the beginning differentiation of the third pair of arms (A_3); the beginning of the typical connection between the fourth and third pair of arms; the developed funnel bonds (Th); form of the funnel retractors (Tr); degree of development of the gills; course of posterior aorta, lateral pallial vein (Vl) and posterior pallial vein (Vp). Note also the gill ligaments, branchial spleen (light, translucent) (Km), afferent and efferent branchial vessels, branchial hearts (Kg), venous appendages (Vs), renal papillae (Ni), origin of the posterior aorta (Ao), hind intestine, anal papilla, ink sac (Tb), vena cava (Vc), base of tentacles (Te), fourth pair of arms (A_4), gill band (Kb).

Rc — origin of cephalopodial retractor in the shell sac; x — probable margin of shell sac (cf. Figure 64 on p. 152); Ms — septum of mantle; Ap — posterior pallial artery; Co — cone; Rs — rostrum.

309 This stage has a dorsal length of the mantle of 9.6 mm and the fins are 2.4 mm long. There are several specimens with a similar habitus, the largest with a mantle length of 10.8 mm and a fin length of 3.6 mm, all of them of uncertain systematic position. If the mantle is 11 mm long, Ancistroteuthis lichtensteini can be distinguished from Onychoteuthis banksi. In Onychoteuthis banksi, for example, the fins are longer than one third of the mantle, in A. lichtensteini they are at first shorter. The gladius of O. banksi is visible dorsally as a sharp line. In A. lichtensteini, this line disappears at first in the middle, then also anteriorly as it is now situated inside the mantle (cf. Figures 150 and 151, which probably represent an Ancistroteuthis). Onychoteuthis with a mantle length of 12 mm has large, differentiated hooks. In Ancistroteuthis, the hooks become differentiated at a slightly later stage. The older stages can thus be determined with certainty, at least in the Mediterranean material and the further development is described here only in general outline. The habitus changes by the lengthening of the arms, the development of the tentacles and the form of the head. The anterior part of the mantle sac becomes more cylindrical and the posterior part longer and more pointed; the fins grow larger and develop "earlobes" and lateral corners (cf. Figure 156). Only a thin mediodorsal line is visible of the gladius which begins near the anterior margin of the mantle and disappears behind the middle of the fins. This line corresponds to the keel of the rhachis or the crest which later develops on it. The flag eventually becomes invisible. Cone and rostrum can still be recognized externally in preserved specimens during the intermediate stages; but they are covered later not by the muscular mantle but by a thick muscular skin, as in the Ommatostrephidae (Figure 107).

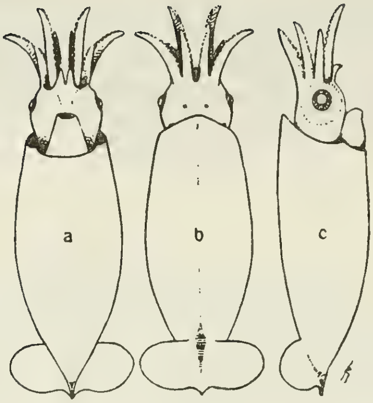

FIGURE 150. Young Onychoteuthis or Ancistroteuthis from the plankton of the Bay of Naples. 6×. The progress in the development of the fins and arm apparatus is distinct.

(310)

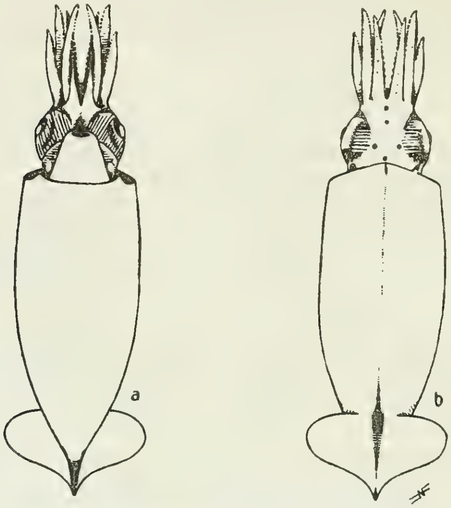

FIGURE 151. Young Ancistroteuthis or Onychoteuthis. 5×. Note the fins, mantle, the dorsally visible gladius, and especially (in ventral view) the cone and rostrum. There are small swimming margins on the distal part of the DL arms.

The fins grow considerably until they occupy at least two thirds of the mantle length at the base. They have at first a rounded, transverse rhomboidal form which may later become pointed posteriorly (Figure 162).
310 The transverse and longitudinal neck folds develop first, the secondary folds later (in the Onychoteuthinae). The olfactory tubercle appears on the third longitudinal fold.

The eyelid develops a sinus and its posterior margin becomes later more or less transverse. The arm apparatus has attained its definitive form. The arms of the third pair are the longest, and the first arms remain the shortest. The typical swimming margins develop. Particularly important is the development of the tentacles. The stalk becomes very long, slightly flattened dorsoventrally, sometimes with edges bordering the inner and outer side; a narrow margin develops along the outer side.

(311)

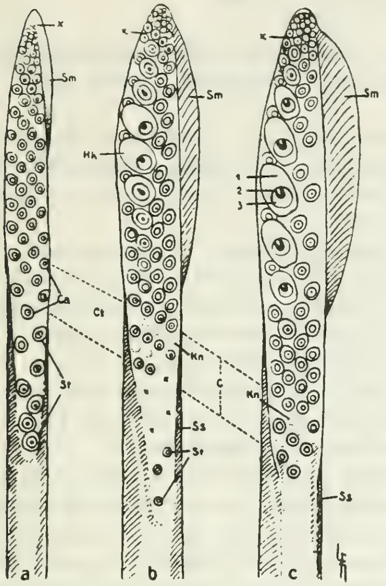

FIGURE 152. Right clubs of older stages of Onychoteuthis banksi. a – 48×; b – 45×; c – 40×. The specimens had a dorsal mantle length of 11, 13 and 15 mm. Note: 1) loss of the biserial stalked suckers (St) (p.310); 2) development of rows of knobs (Kn) between the rows of suckers on the carpal part (C, Ct); 3) the progressing conversion of suckers into hooks (Hk) on the hand part; 4) the development of hooks from parts of the sucker, e.g. hood of hook (1), apex of hook (2), base of hook (3); 5) growth of the swimming margin (Sm); 6) the addition of further suckers (x) to the originally last suckers on the apex.

The typical development of the tentacle club is shown in Figure 152. In younger specimens, slightly older than those described above, there are 4 rows of suckers in the larger distal part of the club and still only 2 rows in the proximal part, of which the first developed and functional suckers are the largest. A swimming margin extends on the dorsal margin of the club, in the distal quarter. Protective margins develop along the whole club in the form of edges. The biserial proximal part corresponds to the "stalk part" of the club and the suckers are later gradually lost, except for a few next to the 4 rows. The first two oblique transverse rows become the carpal part without changing their arrangement; between the rows of suckers develop rows of knobs corresponding to the rows of suckers of the opposite club. The following rows of four form the hand part. The suckers of the ventral middle row are transformed first and correspond to the largest hooks of the club. Their distal outer margin forms a hood over its opening; it becomes larger and a large tooth develops on the "anlage" of the horny ring under the hood which becomes the hook. The conversion extends both
311 proximally and distally, involving also the dorsal median row but not the marginal rows and the short distal part of the club. Strikingly, from the form of the "anlagen" persisting as suckers, it appears as if these were intending a similar conversion, which does not take place. This has also been observed on arms and tentacles of many other Oegopsida.

The luminous organs in the mantle cavity and on the eyeball appear in the same stages (cf. p. 320). The genitalia develop according to the general pattern.

VARIATION OF THE TYPE OF ONYCHOTEUTHIDAE

The Onychoteuthidae are divided into 3 subfamilies with the type genera: Onychia Lesueur, 1821,* Onychoteuthis Lichtenstein, 1818 and Cycloteuthis Joubin, 1919.

Review: a) Onychiinae (= Teleoteuthinae Pfeffer). Gladius Loligo-like, with a wide flag. Occipital folds absent (p. 314). Developed club still with small suckers in the marginal rows and hooks in the median rows. Moroteuthis and Onychia (= Teleoteuthis).

b) Onychoteuthinae. Gladius with rudimentary flag. Occipital folds present on the neck (p. 314). Club of tentacle with hooks in the median rows, the marginal rows disappear after formation of the hooks (the atypical
312 Tetronychoteuthis shows a state of inhibited development with numerous transverse rows of 4 suckers). Genera: Onychoteuthis, Chaunoteuthis, Ancistroteuthis and Tetronychoteuthis.

c) Cycloteuthinae. This subfamily contains only Cycloteuthis sirventi Joubin, 1919, which resembles the Enoploteuthidae.**

Pfeffer places also Lycoteuthis in the Onychoteuthidae because of the similarity of the gladius. But this resemblance is very superficial and does not apply to the recently described related genera Lampadioteuthis and Nematolampas Berry. The gladius of Lycoteuthis would have to resemble the typical gladius of the Teleoteuthinae and not the modified gladius of the Onychoteuthinae if they were closely related; the presence of a small rostrum is a primary character which does not prove a special relationship to the Onychoteuthidae. Lycoteuthis differs from the Onychoteuthidae in a number of distinct characters which it has in common with the Enoploteuthidae (cf. p. 266).

We shall describe below only the Onychoteuthinae, because the other subfamilies do not occur in the Mediterranean.

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* This genus is identical with Teleoteuthis Verrill, 1885, because O. caribaea Les. (Lesueur, Plate 9, Figure 1) is identical with T. caribaea auct. and retains the generic name, after elimination of the species which do not belong there.

** Joubin unites this genus with Lycoteuthis in the family Parateuthidae which are already rejected (p. 266). The gladius is apparently Onychia-like, with a distinct cone and a large rostrum. There is a large luminous organ in the mantle cavity, as in Onychoteuthis banksi (p. 320). Hooks are absent; the suckers bear instead numerous teeth at the distal margin. Median teeth of radula tricuspid.

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